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Habitat selection by American marten (*Martes americana*) at the element, patch and stand scales in a young deciduous forest in northern British Columbia

by

Aswea Dawn Porter

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requirements for the degree of Master of Science

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ABSTRACT

Although animals select habitat across a range of spatial scales, most habitat studies are restricted to the larger scales relevant to management and may overlook selection occurring at smaller scales. At the element scale, animals select specific habitat elements (e.g. logs) for specific activities (e.g. foraging). I conducted a multi-scale study on a population of American marten that, although typically associated with older coniferous forest, was detected in an unusual habitat type; a young deciduous forest. I used radio telemetry and winter snow tracking to identify sites used by marten at the element, patch, and stand scales. At the element scale, marten locations were associated with particular behaviours evident in the snow record. I found that they were most selective during denning and foraging and less so while scent marking and traveling. Alder and willow trees, shrubby ground cover, and deadwood were important at resting dens while logs were important during foraging. At the patch scale, overhead cover was the only significant variable; while at the stand scale, marten appeared to be using their habitat indiscriminately. Young deciduous forests may be suitable for marten if the habitat needed for denning and foraging is present. Habitat selection may not be detected unless studies are conducted across a range of spatial scales that encompass very small scales of selection.

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"Gratitude is one of the least articulate of emotions, especially when it is deep." Felix Frankfurter

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CHAPTER ONE – INTRODUCTION

The forest industry is an important commercial user of British Columbia's boreal forests and contributes substantially to the provincial economy. However, managers must balance the needs of this industry not only with those of other commercial users but also with the public's growing appreciation of wild plants and animals (Adamowicz and Codon 1997). Forest harvesting has the potential to cause habitat loss and fragmentation; processes that have been associated with the decline and local extinction of numerous forest–adapted species (Crooks 2002, Gonzalez and Chaneton 2002). Consequently, forest managers are striving to develop new techniques that will provide more natural conditions and maintain long–term ecosystem integrity (Boutin and Hebert 2002).

For wildlife, the development and success of these new harvesting methods rely upon a thorough understanding of the habitat requirements of target or representative species. We need to identify the specific resources of the forest that permit wildlife to stay in the system at viable population densities and to ensure that these resources are retained throughout the harvesting cycle.

Habitat suitability is ultimately determined by individual animals who decide where to live based on the resources available to them. Habitat selection is usually classified according to a hierarchical scheme and studies tend to focus on a particular scale or to sequentially address a range of scales. First order selection (*sensu* Johnson 1980) can be defined as the selection of the geographical range of the species. Second order, or landscape scale, selection determines the location of the home range. Stand scale, or third order selection, refers to the use of particular habitat types within each home range. Fourth order selection, or patch scale, occurs when animals prefer areas within each of these habitat types whose complexity deviates from the average. More recent classifications (Weir 1995) recognize a fifth or element scale of selection which pertains to the choice of actual eating or resting spots. For many species, it is the occurrence of specific attributes at the elemental scale of selection that determines habitat suitability. Nonetheless, this scale is frequently omitted from habitat selection studies, typically due to logistical constraints.

In order to make clear recommendations to forest managers, the habitat needs of forest–adapted wildlife must be understood all these scales. New vegetation variables may emerge as important at each scale and too strong a focus on any one scale may cause important patterns to be overlooked, or conversely, overemphasized. In addition, an understanding of selection at smaller scales may lend insight into the mechanisms underlying larger scale relationships (Bourgeois 1997, Drew and Bissonette 1997).

This project was designed to investigate stand, patch and element scales of habitat selection using the American marten; an important furbearing species that has been strongly associated with the late successional coniferous forests targeted by industry (e.g. Buskirk and Powell 1994, Drew 1995, Poole and Stanley 1998). This habitat association in combination with large territory requirements and low population density makes the marten particularly sensitive to the effects of habitat fragmentation (Grindal et al. in review). In addition, marten are consistently the most important fur bearing species in British Columbia (British Columbia Ministry of Environment, Lands and Parks 1997). Local populations are currently stable and healthy, but marten have been extirpated from parts of eastern Canada and nine of the northern United States as a result of the combined effects of habitat loss and overtrapping (Thompson 1991).

This study was initiated after an earlier project identified a population of marten living in young deciduous forest in northern British Columbia (Grindal et al. in review; Fig 1.1). This is an uncharacteristic habitat type because marten are believed to be dependent on the dense overhead cover, uneven aged trees, and structural complexity that is most commonly found in older coniferous stands (Buskirk and Powell 1994). Specifically, it is thought that accumulations of coarse woody debris provide marten with access to subnivean small mammal prey in winter, shelter from overhead predators, thermally efficient den sites, and good habitat for their prey (Martin 1987, Coffin 1994, Thompson and Curran 1995, Paragi et al. 1996). In addition, overhead cover and vertical structure, such as well distributed tree stems, are important for predator avoidance and escape (Baker 1992, Coffin 1994, Drew 1995, Potvin et al. 1999). The previous study at this deciduous site did not detect selection for stand type on this study site even though the

locally–developed habitat suitability model gave a low rating to most of the area (Grindal et al. in review). These results did not indicate a clear course of action for managers.

I suggest that this confusion may be an artifact of the scale of study. Animals may be using the habitat in highly selective ways that cannot be detected at the stand scale. Further research is needed to understand how marten respond at the small–scale and how these small–scale results relate to the larger scale studies that are more commonly done. Rigorous small–scale studies have been conducted only for den sites (Buskirk et al. 1989, Chapin et al. 1997, Gilbert et al. 1997, Raphael and Jones 1997, Bull and Heater 2000, Wilbert et al. 2000), and subnivean access sites (a combination of den and foraging locations; Corn and Raphael 1992, Sherburne and Bissonette 1994) leaving the range of other daily activities that may be important for survival unexamined. Further, these studies were not concurrent so that the relative importance of vegetation structure to each is unknown.

I examined habitat selection by marten at the element scale for specific resources and specific activities. I concurrently analyzed habitat selection at the patch and stand scales in order to provide a more complete understanding of the habitat requirements of marten living in young deciduous forest. This information is needed to identify the resources that may be necessary to provide adequate forest structure for marten (Chapin et al. 1997) and will assist managers to balance the needs of commercial forestry operations without compromising the viability of important furbearer populations.

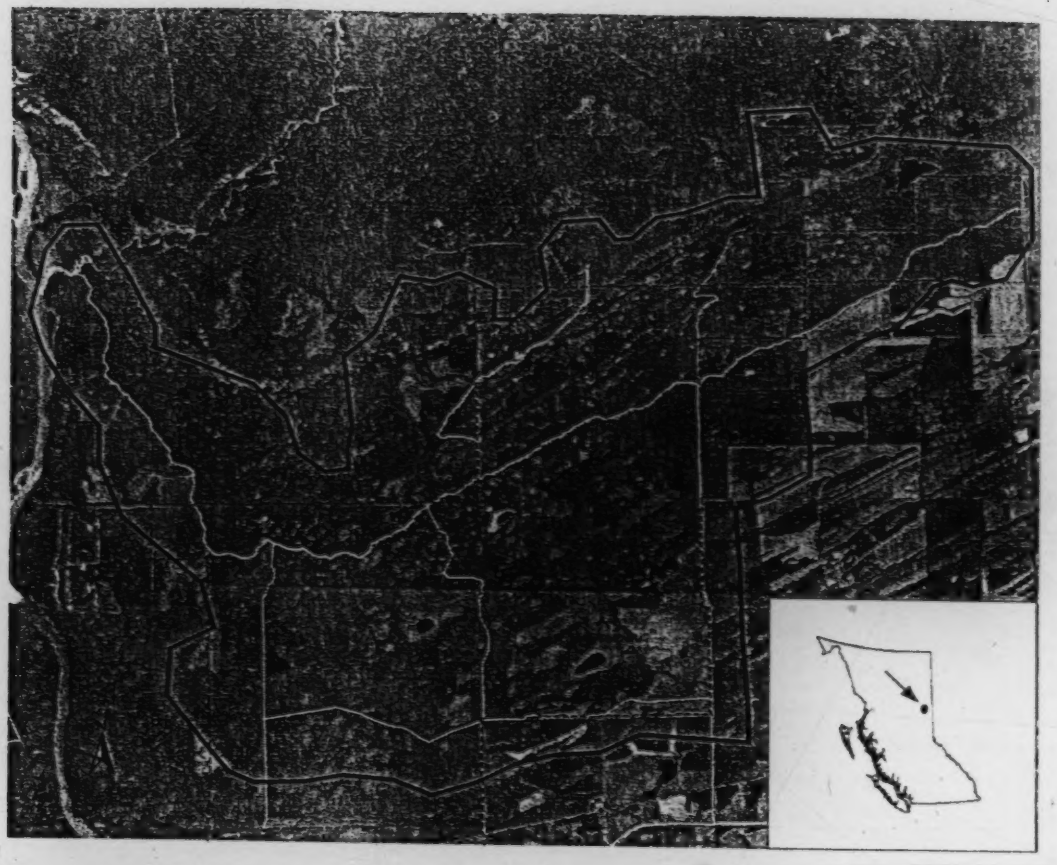

Figure 1.1. The Rice Property study area in northern British Columbia, Canada (scale 1:100000). The background image was derived from orthophotos taken in 1996. The dotted border delineates the Rice Property proper and the solid border outlines the complete study area.

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CHAPTER TWO – HABITAT FOR SPECIFIC ACTIVITIES: SMALL SCALE SELECTION BY AMERICAN MARTEN IN A YOUNG DECIDUOUS FOREST

A growing awareness of the cumulative impacts of land use activities in the boreal forest is challenging managers to develop methods of resource extraction that can conserve species diversity (Boutin and Hebert 2002, Lieffers and Woodard 1997). This is typically approached by focusing on one or several representative species whose requirements must be known in detail. It is expected that protecting these animals will also protect others (Landres et al. 1988). The resulting habitat studies are usually based on the density of animal use at spatial scales that are most relevant to management (e.g. Scott et al. 1998, Castleberry et al. 2001, Lance and Phinney 2001). While these projects produce quality results within a reasonable time frame, they are also limited in the amount of detail they can provide.

I focus on two significant limitations of conventional habitat selection studies in this study. First, treating population density alone as an indicator of habitat quality disregards how animals were using their habitat. Many organisms have been observed to use different habitats for different activities; for example, foraging in forage–rich habitat and resting in sheltered habitat (Lima and Dill 1989, Mysterud et al. 1999). When this detail is not taken into consideration, resources that are used infrequently and/or for specific purposes may not be identified (Johnson 1980, Mysterud and Ims 1998, Mysterud et al. 1999). Second, the management thrust of conventional studies results in a focus on large spatial scales (stand and landscape scales; Johnson 1980), whereas animals frequently select habitat at the scale of individual logs or trees (element scale; Weir 1995, Gaylard and Kerley 2001, Aldredge et al. 2002, McLoughlin et al. 2002). These elemental structures are often left out of the vegetation inventories used for large scale studies. Both sources of heterogeneity may erroneously imply a lack of selectivity (Buskirk and Powell 1994).

I addressed these shortfalls by examining habitat selection for specific activities and specific resources by the American marten. These animals are profitable furbearers and are closely associated with the late successional coniferous forests that are targetted by industry (e.g. Buskirk and Powell 1994, Drew 1995). In particular, marten are believed

to be selective of their habitat in cold weather because they have a high metabolic rate (Iversen 1972) and limited fat reserves (Buskirk et al. 1988). Specifically, it is thought that accumulations of coarse woody debris provide marten with access to subnivean small mammal prey in winter, shelter from overhead predators, thermally efficient den sites, and good habitat for their prey (Martin 1987, Coffin 1994, Thompson and Curran 1995, Paragi et al. 1996). In addition, overhead cover and vertical structure, such as well distributed tree stems, are important for predator avoidance and escape (Baker 1992, Coffin 1994, Drew 1995, Potvin et al. 1999). Still, rigorous studies have been conducted only for resting sites (Gilbert et al. 1997; Raphael and Jones 1997; Chapin et al. 1997; Buskirk et al. 1989; Bull and Heater 2000; Wilbert et al. 2000) and subnivean access sites (a combination of den and foraging locations) (Corn and Raphael 1992; Sherburne and Bissonette 1994), leaving unexamined the range of other daily activities that may be important for survival. Further, these studies were not concurrent so that the relative importance of vegetation structure to each is unknown

This project was initiated to investigate these issues when a population of marten was detected living in a young deciduous forest that seemingly had little in common with older coniferous systems. Most of this area was given a low ranking by the locally developed habitat suitability model (Grindal et al. in review) and two larger scale studies detected only weak patterns of selectivity (Grindal et al. in review; Chapter Three this volume). This discrepancy may be an artifact of the scale of the study or the way in which the animals were using their habitat. While the traditional view of their habitat needs is usually upheld, marten have been found living in some younger forests that retained structural complexity from before the disturbance (Paragi et al. 1996, Chapin et al. 1997). I designed this study to determine if marten were selecting remnant debris at a smaller scale than could be detected in the larger scale analyses and if they were selecting it differently for specific activities: resting, foraging, scent marking and traveling. I identified specific attributes of vegetation structure and prey abundance that were necessary to provide adequate habitat for marten at this small scale. This information may be useful to managers who make land allocation decisions that concern forest–specialized wildlife, and to foresters as they plan their operations to retain features important to these mustelids.

STUDY AREA

This project was conducted on the Rice Property, a parcel of overgrown agricultural land, in Canada's boreal mixedwood forest, 40 km east of Chetwynd, British Columbia, Canada (121° 48' W and 55°42' N). The Property itself covers 5880 ha, but telemetry locations for the study animals extended the study area to approximately 7850 ha. About 5500 ha of this total area is now forested with 90% in primarily deciduous stands (*Populus tremuloides and P. balsamifera*) and the remainder dominated by conifers (*Picea spp., Pinus contorta*). Nearly 65 % of the forest is less than 60 years old and 45 % is between 5 and 25 years of age. There are small stands of mature aspen, mixed aspen/spruce and spruce and tamarack (*Larix larcina*) bogs that were left after the initial clearing. The nonforested land is mainly pastures, clearings and wetlands. The entire area has been fragmented by seismic lines, gravel roads and trails, and clearings related to past agricultural use and timber harvesting. Debris piles and remnant live trees, stumps, logs and snags from the initial clearing are scattered through the younger forest stands.

METHODS

Field work during the winter of 1998 was conducted by Axys Environmental Consulting Ltd. (Axys; Grindal et al. in review). All other field work (winter of 1999, summers of 1999 and 2000) was done by my field assistants and I. Both crews used the same methodology.

Activity site identification

We used radio telemetry to find fresh snow tracks of known individuals. Thirteen marten were radio collared in December of 1998 (2 adult females, 8 adult males, 3 juvenile males) and 18 animals were collared in November of 1999 (7 females [5 adult, 2 juvenile], 11 males [8 adult, 3 juvenile]). Seven individuals were collared in both years. The trapping methodology is described in Chapter Three Methods. We located marten tracks by homing in on their radio signals 12 to 36 hours after snowfall. We then back-tracked and used characteristics of the snow record to identify specific sites where the animal had performed a specific activity.

We identified six different classes of marten activity during back–tracking. These were resting dens, subnivean foraging attempts, scent marks, travel sites, tree climbs, and food remains. Resting dens were places that concealed the animal at the time of location. I was not able to distinguish dens that were used for natal or maternal purposes (see Ruggiero et al. 1998). Subnivean foraging attempts were digs into the snow or places where the tracks disappeared below the snow and fresh tracks emerged elsewhere. Scent marks were either scat or urine deposits. Travel sites were points along a straight section of the track (at least 60 m long and with no turns greater than 45 degrees) with at least 30 m separation from any signs of other activities. I defined travel sites in this way to reduce overlap between activity types. A straight path suggests that an animal is crossing an area, but not choosing it for purposes other than traveling, while a tortuous (characterized by twists and turns) path is a sign of increased use (Bourgeois 1997). Tree climbs were places where marten were apparently arboreal, including evidence of return to the ground (e.g. full length body print deep in snow). These may have been used for foraging or as escape cover. Finally, food remains were usually blood, body parts or eggshell and indicated the location of a successful foraging attempt. All of these marten activity sites were flagged and recorded using a differentially recorded GPS. In total, we identified 471 activity sites in two winters of back–tracking.

The number of marten activity sites that could be subsequently surveyed for habitat characteristics was constrained by personnel and time. With this in mind, I selected a subset of the total sites that was evenly distributed over all individual marten and all sampling days. This maximized the range of variation that could be accommodated and prevented any particular animal from having an overly strong influence on the results. Each animal had three replicates of each activity type. When more than three sites were available for an animal, the ones to be surveyed were chosen randomly from two or more tracking sessions. I excluded any individual with less than three replicates for a particular activity from that analysis. I did not sample activity sites if they fell within two sample plots of another sampled site. Finally, I excluded two activities, tree climbs and prey remains, from the analysis because of small sample size. This resulted in a sample of 189 activity sites which included 36 resting dens, 51 subnivean investigations, 45 scent marks and 57 travel sites.

I paired each of these activity sites with a random site that was intended to provide a measure of the habitat available within that patch of forest. The random sites were centered a standard 30 m from the activity sites in a random direction. The close proximity was necessary so that used habitat could be compared to available habitat at the element scale. I chose this specific distance for two reasons. First, marten appear to change activities within a limited area. Preliminary analysis of the first season of backtracking data showed that 20% of activity sites were within 30 m of another activity site of a different type. Bourgeois (1997) also found that marten responded to specific habitat structures every 30.9 m of track. Second, this was the minimum separation for my intended vegetation sample plot of 15 m diameter that would avoid resampling vegetation variables (such as long logs) in both the random and used sites.

Habitat sampling

We conducted vegetation (1999, 2000) and small mammal prey (1999 only) inventories in order to identify the habitat characteristics that were associated with each activity type. These surveys were conducted within 15 m diameter circular plots. I chose 15 m as an appropriate size to focus on microhabitat features while ensuring that the actual activity sites were included in the assessment. There was some ambiguity about the position of the sites that were located during the winter 1998/99. This was because the data collected during the Axys study were originally intended for use in a different context. As a result the flagging on approximately 75% of the marten activity sites was removed after the sites were recorded with GPS. We had to relocate these sites the following summer using a real–time differentially corrected GPS. This unit was accurate to within 5 m resulting in a cumulative possible inaccuracy of 10 m (five m for the initial location plus five m for the relocation) for the center of the plot.

The vegetation sampling protocol was adapted from standard government procedures to increase management relevance for this site and species (British Columbia Ministry of Forests 2001). Mainly, this involved using a 15 m circular plot, instead of the standard two 24 m perpendicular transects, in order to capture information over a smaller spatial scale. We measured 40 vegetation characteristics independent variables for analysis (Table 2.1). We assessed overhead cover before leaf–out using a concave densiometer

held in a kneeling position to approximate marten head height in winter. All features that could provide cover (e.g. tree trunks, logs, forest canopy) were included in this measurement. We averaged the final value from readings taken at three standard locations within the plot. After snowmelt, logs, snags and stumps were counted, measured for width at a standard location and assigned a decay class (five classes for logs and stumps, three classes for snags). In addition, we classified logs as down or suspended and measured the angle with respect to the horizontal with a clinometer for all suspended pieces. We then assigned a height class to the stumps (short, medium, or tall). We counted live trees in a randomly chosen quarter plot or two opposing quarter plots depending on our assessment of the uniformity of the site. The partial count was multiplied to estimate the density of trees in the plot. We also identified trees to genus and measured their diameter at breast height. Root mounds from fallen trees were counted and their length and width was estimated (±10 cm). Debris piles were counted, assigned to a decay class, and measured for length, width and height (± 25 cm). Finally, we estimated ground cover as percent cover of shrubs, herbs and grass in a 1 x 1 m quadrat using the Braun–Blanquet system of classification (Mueller–Dombois and Ellenberg 1974). We took three measurements at separate locations within the plot and averaged the results.

Small mammals are the preferred subnivean prey of marten (Martin 1994). We surveyed their abundance at 93 of the activity sites (plus paired random sites), including 33 subnivean investigations, between August 15th and September 25th 1999. We set five live traps at each site: one multiple capture trap (Tincat™) in the center and four single capture traps (Longworth™) at 3.5 m spacing in each of the cardinal directions. These traps were prebaited in a locked, open position for three nights and then set for two nights. We identified all captures by species, weighed them and then released them. I did not continue this survey for the activity sites that were identified in the subsequent winter (1999–2000) because preliminary analyses did not detect any signficiant differences between used and random sites for the small mammal variables (see Results).

Statistical Analysis

I used one–to–one matched case–control multiple logistic regression modelling to identify the habitat characteristics that were important to marten. Although logistic regression response variables are typically binary and mutually exclusive, this can include the classification of habitat as used (activity sites) or available (Manley et al. 1993). Logistic regression has several advantages over more traditional habitat analyses. In particular, it (1) is quantitative and predictive, (2) can be used for continuous and categorical independent variables, and (3) allows assessment of linear, non–linear and interaction effects. One–to–one matched case–control logistic regression (Schlesselman 1982, Hosmer and Lemeshow 1989) has these same capabilities but can also remove variability that could not be assessed otherwise by matching the sample sites by a common variable believed to be associated with the outcome. In this study, activity sites were matched with their paired random sites in order to emphasize within–site variability (i.e. that present between paired random and used sites) while minimizing among–site variability (i.e. that occurring among sites [random or used] in different forest types). This technique can be thought of as a functional equivalent of a paired t–test for multivariate analyses. Although it is infrequently used in wildlife studies, it is a common tool for medical scientists.

I developed four multiple logistic regression models (one model for each activity type) using the one–to–one matched case–control technique. I performed these analyses using SPSS (Version 9.0, SPSS Inc. 1998) and S–Plus 2000 (Professional release 1, Mathsoft Inc. 1998–99) software. In all cases I followed a series of model–building steps that were derived from multiple sources:

1) I conducted univariate regressions on all the habitat variables to create a subset of the most significant variables. These were then used as candidates for inclusion in the multivariate model (Hosmer and Lemeshow 1989). I considered a variable to be significant enough to include in this subset if the log–likelihood test produced a P value < 0.25. Hosmer and Lemeshow (1989) recommend using this large P value to retain variables that may become significant only after the effects of other variables have been taken into account in the multivariate analysis. I discuss in the text those variables that

were significiant in the univariate regressions at $P \leq 0.1$ and which were not included in the multivariate regressions. Finally, univariate parameters were reported as significant only if the magnitude of their Wald value was ≥ 1. The Wald statistic is not recommended as a test of significance (Hosmer and Lemeshow 1989) but was used as a diagnostic of a disproportionately large standard error of the coefficient.

2) I built trial multivariate models using the candidate variables identified in the univariate analyses. When these indicated that some highly correlated variables (Spearman's rho < 0.5) would be included, I combined the related variables with principle components analysis. I then used the resulting components as candidate variables for logistic regression in place of the initial variables they represented (Table 3). This precluded the subjective removal of variables and allowed for a more complete interpretation of habitat structure present on the study site.

3) I then constructed the final multivariate models. I first added the main linear effects using a forward stepwise procedure based on the log–likelihood ratio with $\alpha = 0.1$ for inclusion and 0.15 for retention (Hosmer and Lemeshow 1989). Again, variables were removed if the magnitude of their Wald value was less than 1. Secondly, I added quadratic variables if both the x and x^2 values satisfied screening criteria (log likelihood $P < 0.1$, Wald ≥ 1). I limited the assessment of non–linear effects to quadratics because of their simplicity and plausible biological relevance. Finally, I tested two–way interactions for all the parameters already in the model plus those related to overhead cover, prey habitat, and medium–to–large diameter coarse woody debris. This subset was chosen for its biological relevance because the complete set of two–way interactions for 40 independent variables was too large to consider. I included the interactions if they provided a significant improvement in fit ($P < 0.1$) and were biologically interpretable.

4) I calculated three statistics to assess the overall performance of the final models. I used the log–likelihood ratio test and a measure of the proportion of explained variance analogous to linear regression (R^2_L) to determine if the model predicted the outcome variable better than a null model (Hosmer and Lemeshow 1989). These are relative measures that compare fitted values under two models. Conversely, goodness–of–fit is

used to determine if the predicted values are an accurate estimation of the observed values in an absolute sense. This is harder to determine with matched case–control logistic regression because the response variable equals one for all strata (Hosmer and Lemeshow 1989). Therefore, I ran the final models with regular logistic regression and calculated the Hosmer and Lemeshow goodness–of–fit statistic as a conservative estimate of model fit (Hosmer and Lemeshow 1989). It is conservative because the desired partitioning of variance within and among pairs of points is not possible, increasing the likelihood of Type 2 statistical errors.

These four steps were used to examine the vegetation variables, but only the initial step, the univariate analysis, could be applied to the small mammal data. This is because we collected this data on a subset of the activity sites that we had sampled for vegetation characteristics. I organized the small mammal data into four continuous variables: total captures, average weight (g), number of red backed voles *(Clethrionomys gapperi)*, and number of deer mice *(Peromyscus maniculatus)*. Red backed voles and deer mice were the only abundant species on the study site (see Results). Again, I used one–to–one matched case–control logistic regression to determine the importance of each variable. I did this separately for the subnivean investigations (N=33) and for the combined activity sites (N=93). I assessed both linear and quadratic relationships with the outcome. I considered variables to be significant if they met the conditions listed above for the univariate analysis of vegetation data.

RESULTS

Resting dens

The multiple logistic regression model for resting dens was highly significant ($P < 0.001$), explained 68 % of the deviance in the data, and fit adequately according to the Hosmer and Lemeshow goodness–of–fit criterion ($P = 0.18$; Table 2.2). This indicates that marten were very selective of their resting dens within a 30 m area. The final model was constructed from a subset of 21 candidate variables that differed between actual and random sites ($P < 0.25$) in preliminary univariate analyses (Table 2.3A). Nine of the candidate variables were included in the final model (Table 2.4A) and an additional five

were significant enough ($P < 0.1$) to be discussed in the text. Three of the variables in the final model were represented by one principle component factor and thus the final degrees of freedom were seven rather than nine (Table 2.5A).

Of the variables that were detected to influence choice of resting den, the most significant were shrubby trees and shrubby ground cover. Marten tended to use sites with 130 % more shrubby trees and 32 % more shrubby ground cover than was available randomly in the habitat. In addition, the shrubby ground cover was significant in a two–way interaction variable with undecayed logs. This interaction suggests that marten avoided shrubby areas if they contain undecayed logs (Fig. 2.1A). Both of these variables provide shelter and the animals may have been able to subsitute them for one another. Marten also used sites with 56 % less grassy ground cover and 35 % fewer thin trees on average than was available randomly. All other significant variables were related to deadwood (logs, stumps and snags). Marten selected for a principle component that represented increasing numbers of moderately decayed snags of all diameter classes (Table 2.5A). Of these, they used sites with 110 % more moderately decayed snags, 152 % more medium and wide diameter snags and 46 % more thin snags than were available randomly on average. Further, resting dens tended to have 300 % more undecayed logs and 34 % more wide diameter logs than were randomly available. Finally, moderately decayed stumps were 50 % more likely while short stumps were 32% less likely to be present at used sites than at available sites. In sum, the study animals seemed to prefer the shelter close to the ground that would be provided by alder and willow trees as well as by shrubby ground cover and the branches from freshly fallen logs. They tended to avoid features that did not provide that protection such as grassy ground cover and thin trees. Deadwood was important including material that was either undecayed or moderately decayed and had a range of diameter classes.

Foraging sites

Marten were selective of their foraging sites at the element scale. The final multivariate model was highly significant ($P < 0.001$) and fit the data adequately ($P = 0.2$). It explained 54 % of the variability in the data which is slightly less than was explained by the resting den model (Table 2.2). Based on the univariate analyses, twelve independent

variables were included in the candidate subset that was used to develop the multivariate model (Table 2.3B). Five correlated variables related to logs were combined into one principle component factor and four variables related to stumps were combined into two other principle component factors (Tables 2.5B and C). Thus nine variables were represented by the final regression, but the principle component factors reduced the degrees of freedom to five from nine (Table 2.4B).

Marten selected for a large number of variables related to logs. They tended to forage at sites with 39 % more wide logs and 35 % more total log debris than were available at random. They also selected three variables related to logs that were represented by a principle component factor (Table 2.5B). This suggests that marten tended to forage at sites with 14 % more medium diameter logs, 44 % more undecayed logs and 27 % more suspended logs than were available randomly. Marten avoided stumps if they were tall, thin and moderately decayed (PCA factor 1; Table 2.5C) but selected stumps if they were wide (PCA factor 2). Used sites had an average of 54 % fewer thin stumps and 40 % more wide stumps than were available at random in the habitat. The tall, thin and moderately decayed stumps were also significant in an interaction with undecayed snags which suggests that marten avoided stumps with these characteristics even more strongly as the density of this type of snag increased (Fig. 2.1B). Thus deadwood, especially logs and wide stumps were important during foraging.

Scent marks

The final multivariate model for scent marking was significant ($P = 0.006$), fit the data adquately ($P = 0.778$), and explained 20 % of the deviation in the data (Table 2.2). This indicates that marten selected habitat for scent marking at the 30 m, elemental scale, but they did this with less specificity than they showed for resting or foraging. Seven candidate variables were selected in the preliminary univariate analyses (Table 2.3C) and the three most significant of these were included in the final model (Table 2.4C). The sites that marten used for scent marking contained 130 % more wide trees and 28 % more thin trees on average than did randomly available habitat. Marten also tended to scent mark in sites with 23 % more undecayed logs than were randomly available.

Travel sites

Perhaps predictably, the marten showed less selectivity for their travel sites. This model was highly significant ($P = 0.003$) and had an adequate fit to the data ($P = 0.83$), but like the scent marking model, explained only 24 % of the deviance in the data (Table 2.2). The final model was built from a candidate subset of nine variables that met the significance criteria in the preliminary univariate analyses (Table 2.3D). Three of these variables were combined into a principle component factor (Table 2.5D). Thus the final model represented seven habitat variables, but required only four degrees of freedom (Table 2.4D).

Marten tended to travel through sites that had 92 % more medium diameter (10–25 cm) trees than were available at random. They selected snags if they were thin and undecayed (PCA factor 1; Table 2.5D); using sites with 60 % more thin and 66 % more undecayed snags than were randomly available in the habitat. Conversely, marten avoided moderately decayed deadwood during traveling and used sites tended to have 26 % fewer stumps of decay class four and 14 % fewer logs of decay class three than were available on average.

Small mammals

During 1860 trap nights, we caught 1100 small mammals. Six species were represented, but 96 % of the captures were of three important prey species for marten. These included red backed voles (*Clethrionomys gapperi*, 34.57 captures/100 trap nights, 15 g mean weight), meadow voles (*Microtus pennsylvanicus*, 11.83 captures/100 trap nights, 17 g mean weight), and deer mice (*Peromyscus maniculatus*, 10.59 captures/100 trap nights, 16 g mean weight). I tested four independent variables to see if they influenced habitat selection by marten for either general habitat use (combined activity sites) or for foraging in particular: total captures of small mammals, mean weight (g) of small mammals, number of red backed voles, and number of deer mice. None of these variables were significant in either analysis. The largest effect size was a 15 % drop in the average number of deer mice at sites used by marten compared to random sites and no other effect size was greater than 10 %.

DISCUSSION

Two major patterns emerged from the element scale analysis. First, marten selected their habitat differently for each activity type. Of the habitat variables incorporated into the four activity–specific models, only one fifth were selected or avoided in a similar manner for more than one purpose. This suggests that each activity is performed more effectively in a specific habitat and that animals choose these specific habitats at a very small scale. Second, marten were more selective for some activities than for others. They selected most strongly for resting dens, followed by subnivean foraging sites, and were less selective of their scent mark locations and, predictably, of their travel sites. This order of specificity likely reflects the fitness consequences of selecting particular habitat for each activity. An examination of the specific resources that were selected and their plausible biological interpretations may reveal how these patterns emerged.

I detected the strongest selection for resting dens, which is not surprising given the fitness implications of choosing a sheltered place to rest in winter. A good den can provide protection from predators and substantially reduce thermoregulatory costs in cold weather (Buskirk 1984). Marten are reported to conserve energy by increasing the amount of time spent in their dens as the ambient temperature drops (Buskirk et al. 1988, Thompson and Colgan 1994).

Marten selected resting dens with wide diameter deadwood (logs and snags) and moderately decayed deadwood (stumps and snags). This pattern is in agreement with other work which has associated dens with a number of structural features that share these diameter and decay stage characteristics, such as logs, stumps, rootballs, snags, tip up mounds, and squirrel middens (see e.g. Chapin et al. 1997, Gilbert et al. 1997, Raphael and Jones 1997, Bull and Heater 2000, Wilbert et al. 2000). These features are large enough to accommodate the marten and also have a low thermal conductance that allows the animal to warm the space with emitted body heat (Buskirk 1984, Buskirk et al. 1989). Other variables that were important for marten at resting dens include shrubby ground cover and freshly fallen logs which retained branches and foliage. These structures can suspend snow off of the ground, block wind (Chesterman and Stelfox 1995), and provide cover close to the ground that serves as shelter from predation. This interpretation is further supported by their avoidance

of grass cover, which dies back during the winter and cannot serve these functions. Den sites have been associated with shrubby ground cover and undecayed logs in previous studies (Martin 1987, Wilbert et al. 2000). Marten also selected for shrubby (willow and alder) trees at resting dens. These trees grow commonly along the edges of clearings or wetlands (Johnson et al. 1995) and might provide den sites with prey–rich edge habitats (Menzel et al. 1999). Older willows can also exhibit complex shapes with many live and dead stems as well as debris on the ground. Possibly this structure functioned similarly to structure in an older forest and sheltered the marten from predation and inclement weather. Finally, grizzly bears have been observed to den under shrubby trees because the roots provide support for the ceiling of dens (McLoughlin et al. 2002). Shrubby trees and shrubby ground cover may serve a similar function for marten resting dens.

It is more difficult to interpret the selection that was detected at resting dens for thin trees and thin snags. The thin trees and snags were too thin (< 10 cm) to have cavities of sufficient size for marten. Thin snags were significantly correlated with thin trees (Spearman's rho = 0.23), suggesting that they may be associated with the self – thinning of young forest stands. Possibly this young forest was sufficiently dense to provide shelter to the resting site.

Second in magnitude only to resting dens, marten also showed strong selection for their foraging sites. Efficient foraging has fitness benefits because it reduces the amount of time spent away from shelter. Marten, like other mustelids, have long and thin bodies that are suited to hunting subnivean small mammal prey. They must leave their dens frequently (at least once per day) to forage because they also have a high basal metabolic rate (Iversen 1972) and insignificant fat reserves (Buskirk and Harlow 1989, Harlow 1994). The study animals selected more variables related to logs for foraging than they did for any other activity type. This is likely because logs create breaks in the snow for subnivean access or for assessing the availability of prey (Corn and Raphael 1992, Bourgeois 1997), provide protection from predators while foraging (Paragi et al. 1996, Bourgeois 1997), and form suitable habitat for red backed voles and deer mice (Coffin 1994, Hargis and McCullough 1984, Tallmon and Mills 1994, Martin 1994). These were the two most abundant prey species on the Rice Property during this project and voles, in

particular, are preferred by marten (Martin 1994). Meadow voles were also detected on the study site and their preference for grassy habitats (Adler and Wilson 1989, Simon et al. 1999) may explain why marten selected for grass cover during foraging even though they avoided it during resting.

While logs were important for foraging, some other types of deadwood were avoided. The study animals avoided stumps if they were tall, thin and moderately decayed. A significant interaction variable suggested that they avoided these stumps even more strongly at sites with more undecayed snags. This may be because these stumps and snags have characteristics that are not useful for foraging and tend to occur in places that do not have the more beneficial habitat structures that the animals selected for. Both were upright features with a thin diameter and only a small amount of surface area in contact with the ground. These characteristics result in less small mammal habitat than do the wide diameter stumps and the medium– to wide–diameter logs that were selected for. In addition, thin–diameter deadwood is characteristic of younger forests and may not occur frequently in the same area as the wider structures common to older forests.

The marten showed significant selection for scent mark sites, although less than for resting and foraging sites. Scent marking is thought to be a primary form of communication and territorial marking for mustelids (Pullianen 1982, Hutchings and White 2000, Heath et al. 2001). While both these functions have fitness consequences, it is probable that they are not as time consuming or critical as resting or foraging. Thompson and Colgan (1994) have suggested that scent marking may even be suspended in colder weather when leaving the den is more energetically expensive. Animals, including marten, are usually thought to scent mark in obvious locations where their deposits are likely to be encountered (Pulliainen 1982, Hargis and McCullough 1984, Roberts 1997, Carranza and Mateos-Quesada 2001,). However, the study animals selected for only one element that might be interpreted as serving this function (moderately decayed logs) and it explained only a small amount of the variability in the data. They selected more strongly for thin and wide diameter trees for scent marking, which might reflect a tendency for marten to stop when they were in forested rather than exposed areas.

Marten displayed approximately the same amount of selection for travel sites as they did for scent marks. Animals are probably under pressure to minimize the time they spend traveling, rather than foraging or resting, and they may select a quick and easy path to move among these sites. This might explain why marten have been found to move directly across clearcuts (Soutiere 1979). Conversely, exposure to predation has been observed to be higher for animals that are mobile (Daly et al. 1990, Sakai and Noon 1997) and taking a direct route may increase this risk. Marten have been observed to move preferentially towards trees and logs (Bourgeois 1997) and to either circumvent or use forested corridors to cross open areas (Gyug 1994, Hargis and McCullough 1984). The study animals may have selected less strongly for this activity because they were balancing these competing factors. Another explanation for the lower selectivity detected for traveling is that marten may have assessed habitat more strongly at a larger scale. Particular habitat elements (e.g. a tree or log) may not be as influential if they are passed by quickly. This larger scale selection may also explain some of the remnant variablity for the other activity types.

The ability of animals to travel through unfavourable habitat has received attention in relation to the effects of habitat fragmentation (Beier 1995, Gillis and Nams 1998, Norris and Stutchbury 2001, Belisle and St. Clair 2002). The reduced selectivity that I detected at travel sites suggests that marten were able to move through habitats that they did not use for resting or foraging. Thus, disconnected areas of higher quality habitat may combine to support healthy individuals. This vagility and flexibility may reduce the impact of habitat fragmentation caused by land use activities such as forestry. However, the necessary number, size and distribution of the habitat elements that are important for foraging and resting are yet to be determined. These spatial characteristics affect patterns of habitat occupancy at the landscape scale (Hargis et al. 1999, Potvin et al. 1999, Raphael et al. 2002) and are likely to do so at the element scale as well.

Prey availability likely has a strong influence on habitat selection by carnivores (Thompson and Colgan 1994, Thompson and Curran 1995, Lachowski 1997, Ray 1998, Jones and Barmuta 2000). and small mammal biomass has been found to be an indicator of subniveau access site selection by marten (Sherburne and Bissonette 1994). However, in this study small mammal prey was not observed to influence habitat use by marten either for

subnivean foraging, or for general habitat use at the element scale. Although the number of captures on the Rice Property seemed to be high in relation to other studies (Koehler and Hornocker 1977, Koehler et al. 1990, Thompson and Curran 1995, Waters and Zabel 1998, Potvin et al. 1999, Bowman et al. 2000), this comparison is confounded by different trapping methodologies. It is likely that in this study the small mammals were lured towards the baited traps from surrounding more favourable habitat (R. Moses, University of Alberta, personal communication). This may be responsible for the high numbers of animals detected and for the lack of differentiation between used and available sites, both of which may have sometimes been situated within a single animal's range of bait detection. Small mammals have been censused successfully at the element scale in the past using a baited technique (Sherburne and Bissonette 1994), but movement tests in my study site revealed that a single animal can easily cover the 30 m distance between random and activity sites within a day (Porter, unpublished data). For this reason, I suspended small mammal sampling after one season and directed my effort towards a larger scale, patch scale inventory (Chapter Three this volume).

It is clear that this project identified specific habitat structures that were important to the Rice Property marten and some of these features were associated with particular behaviours. Thus, it appears that the unexpected occurrence of marten at this site can be partially explained by the highly selective use of specific habitat elements that are scattered throughout their home ranges. Despite this positive main conclusion, there were important biological inconsistencies in the selected terms. For instance, moderately decayed stumps and snags were important to resting marten, but moderately decayed logs were not. For scent marking, thin and wide trees were selected while medium diameter trees were not. This may have occurred for two reasons. The first is related to the distinction between selection and availability. Because this study was designed to detect resources that the marten used disproportionately to their availability (*sensu* Manley et al. 1993), only resources that are both used frequently *and* not readily available can be selected. Similarly, only resources that are seldom used and yet abundantly available can be avoided. This important distinction means that those habitat variables that are used in proportion to their availability will not be identified as selected even if they are both used and critical for survival. A second potential reason for these biological inconsistencies stems from the

artifactual results that may occur when high inter–site variability is combined with a liberal alpha value for significance. I chose a liberal alpha ($P = 0.1$) because my sample size was small and this paper may have implications for conservation and for management. In this situation, the consequences of overlooking an important variable for marten (Type 2 error) are greater than the consequences of including extraneous variables (Type 1 error).

The above limitations were inherent in the method of analysis that I chose to use. However, other shortfalls arose because logistical constraints prevented me from investigating habitat selection with the degree of detail that I had originally intended. First, the microscale focus may not have been fine enough to resolve even smaller scale patterns of selection. For example, den sites are often broken down into resting, natal and maternal dens (e.g. Ruggiero et al. 1998), but these were considered equivalent in this project. Natal and maternal dens in particular are important to the successful raising of young but the habitat elements that are important for these activities may not have been detected if marten selected habitat differently or less specifically for resting dens alone. Scent marks provide another example as they were a combination of urine and scat deposits; either one of these marks may be randomly placed or used to communicate different information.

A second logistical limitation is that I combined data that were collected for different individual animals and during two separate winter field seasons in order to increase my sample size within analyses. The characteristics of snow, such as depth and crustiness, can affect the choice of appropriate habitat (Brown and Theberge 1990, Karlsson and Potapov 1998, Selas 2001). For example, the availability of small mammal prey to predators may decrease as snow accumulates (Selas 2001, Hansson 2002). Because the winter of 1990-2000 had less snowfall than the winter of 1998-1999 (~0.25 m versus ~0.5 m), I may not have identified habitat elements that were important during more extreme conditions. The combination of sex and age classes of marten may have added further variability. Females of many species may be very selective of their habitat because of the demands associated with raising young (McShea et al 2002, Revilla and Palomares 2002). Female marten have been found to maintain smaller home ranges than males (Buskirk and Powell 1994, Paragi e al. 1996) which suggests that this pattern also applies to my study species. Similarly, adult animals, including marten, may be more likely to reside in higher quality habitats than are

juvenile animals (Smith et al. 1993, Buskirk and Powell 1994, Coffin 1994). The habitat elements selected by adult female animals are probably most important for reproductive success. However, these elements may not have been identified in this study because of the variability introduced by juveniles and males. For these reasons, I suggest that it would be profitable to increase the resolution of habitat studies beyond what I have presented here. This might include identifying the habitat requirements of more specific activities for individual age and sex classes, especially during harsh climatic conditions.

In summary, this project identified specific habitat elements that were important for marten while resting, foraging, scent marking and traveling. The study animals were found to select different habitat elements for each activity. Further, they were more selective of the habitat they used for resting and foraging than they were for scent marking and traveling. This small scale and detailed selection may explain why marten are able to survive in a young deciduous forest. While most habitat work is done at large scales of analysis, this project shows that the element scale can provide important additional information; in fact, assessment at this scale may be capable of resolving selection that is missed by studies at larger scales. Future research could increase the level of detail beyond that chosen for this study, perhaps by focusing on selection by individual animals and the structures they use for different activities. Futher work might also determine the necessary number and spatial distribution of resting and foraging sites that must be maintained within an animal's home range.

Table 2.1. Habitat variables measured at sites used by American marten for resting, foraging, scent marking and traveling as well as at paired random sites in a young deciduous forest in northern British Columbia. Unless otherwise indicated, a total count of these variables was made within the plot.

Variable	Definition
Logs	diameter > 7.5 cm at widest point, length ≥ 1 m
thin, medium, wide	thin (< 10 cm), medium (10–25 cm) and wide (> 25 cm) diameter at widest point
grounded	laying flat on the ground
suspended	suspended off of the ground
angle	average angle to the horizontal of suspended logs
decay (class 1–5)	1 (fresh) to 5 (completely rotten)
Stumps	top diameter ≥ 4 cm, height ≤ 1.5 m
thin, medium, wide	thin (< 10 cm), medium (10–25 cm) and wide (> 25 cm) diameter across the top
short, medium, high	short (< 0.5 m), medium (0.5 m – 1.0 m), and high (1.0 m – 1.5 m)
decay (class 1–5)	I (fresh) – 5 (completely rotten)
Snags	standing dead tree, height > 2 m, diameter at breast height ≥ 4 cm
thin, medium – wide	thin (< 10 cm), or combined medium and wide (> 10 cm) diameter at breast height
decay (class 3/4, 5/6)	combined decay classes from 3 (fresh) to 6 (rotten)
Trees	height > 2 m, dbh ≥ 4 cm
thin, medium, wide	thin (<10 cm), med (10–25 cm) and wide (> 25 cm) diameter at breast height
deciduous, coniferous, shrubby	deciduous (*Populus, Betula*), coniferous (*Pinus, Picea*) and shrub (*Alnus, Salix*) form trees
Grass, shrub, herb	average percent cover ground cover
Rootballs	mound of dirt and root at the base of a fallen tree
Overhead cover	% cover measured at 1 m above ground

Table 2.2. Overall model fit diagnostics for 1–1 matched case–control multiple logistic regressions that explain patterns of resting, foraging, scent marking and traveling by American marten in a young deciduous forest in northern British Columbia.

	–2 Log Likelihood	Deviance	P^a	C	P^b	R^2_L
Resting dens	16.06	33.86	<0.001	11.43	0.18	0.68
Subnivean foraging sites	41.86	28.84	<0.001	11.03	0.20	0.41
Scent marks	49.79	12.59	0.01	4.81	0.78	0.20
Travel sites	60.28	18.74	0.001	4.29	0.83	0.24

[a] Significance of the log likelihood value that was used to assess how much better the multivariate model predicted the outcome variable than did the null model. [b] Significance of the Hosmer and Lemeshow goodness–of–fit statistic (C) that was used to assess how well the multivariate model predicted the outcome value in an absolute sense. For this second test, models are considered to be adequate when $P > 0.05$

Table 2.3. The mean, standard error, coefficient and model diagnostics of habitat variables found to have a linear relationship with the outcome in 1–1 matched case–control univariate logistic regressions that were performed to select a candidate set of variables prior to building multivariate regression models. These variables explain patterns of resting, foraging, scent marking and traveling by American marten in a young deciduous forest in northern British Columbia.

A. Resting dens

Variable	Avail. mean	SE	Used mean	SE	Correlate group[a]	Coeff.	Wald	P^b
Trees shrubby	8.85	2.13	20.44	4.71		0.05	2.28	0.00
Shrub cover %	26.36	2.35	34.91	2.28		0.06	2.21	0.00
Snags decay 5/6	0.75	0.25	1.58	0.31	3 4 5	0.60	2.18	0.01
Snags	1.81	0.34	2.97	0.62	1 2 3	0.34	1.89	0.02
Grass cover %	8.80	2.51	3.89	0.88		–0.09	–1.58	0.02
Rootballs	0.22	0.07	0.50	0.12		1.07	1.98	0.03
Snags medium/wide	0.31	0.13	0.78	0.19	2 4	0.63	1.89	0.03
Logs decay 2	3.61	0.57	5.03	0.82	8	0.16	1.72	0.05
Logs wide	2.31	0.38	3.14	0.43		0.23	1.65	0.07
Logs decay 1	0.06	0.04	0.25	0.10		1.03	1.53	0.07
Trees thin	11.00	2.01	7.19	1.33	6	–0.05	–1.63	0.08
Snags thin	1.50	0.31	2.19	0.55	1 5	0.26	1.48	0.09
Stumps decay 3	1.08	0.20	1.61	0.35		0.25	1.29	0.14
Stumps short	1.36	0.22	0.92	0.23		–0.27	–1.36	0.15
Trees decid.	36.79	7.00	27.48	4.63	6	–0.01	–1.34	0.16
Logs decay 5	2.14	0.39	1.56	0.31		–0.19	–1.29	0.17
Stumps decay 2	0.81	0.31	0.42	0.13		–0.29	–1.14	0.18
Logs	16.03	1.91	19.28	2.32	7	0.03	1.22	0.19
Logs suspended	4.47	0.81	5.61	0.76	7 8	0.07	1.15	0.23
Stumps tall	0.69	0.15	1.03	0.24		0.25	1.14	0.23
Logs thin	2.56	0.47	2.00	0.42	8	–0.14	–1.14	0.24

B. Subnivean foraging sites

Variable	Avail. mean	SE	Used mean	SE	Correlate group[a]	Coeff.	Wald	P^b
Logs wide	1.69	0.25	2.35	0.30		0.29	1.96	0.03
Stumps thin	1.33	0.44	0.61	0.17		–0.35	–1.70	0.03
Stumps tall	0.57	0.14	0.39	0.10	2	–1.08	–1.94	0.03
Stumps decay 3	0.94	0.16	0.59	0.13	2	–0.58	–2.03	0.03
Snags decay 3/4	0.86	0.21	1.39	0.24		0.33	1.87	0.04
Logs and debris	15.33	1.73	20.69	2.27	1 4	0.03	1.69	0.05
Logs decay 2	4.24	0.70	6.14	1.24	1 3 5	0.07	1.40	0.10
Logs angle	3.56	0.62	4.35	0.60	3	0.12	1.5	0.12
Stumps wide	0.96	0.23	1.33	0.27		0.27	1.44	0.12
Logs	13.88	1.38	16.33	1.46	4 5	0.04	1.37	0.14
Canopy	56.42	1.98	59.75	2.08		0.02	1.39	0.15
Logs suspended	5.33	0.94	6.78	1.09	3 4	0.05	1.12	0.21

C. Scent marks

Variable	Avail. mean	SE	Used mean	SE	Correlate group[a]	Coeff.	Wald	P^b
Trees wide	0.31	0.11	0.71	0.22	1	0.89	1.72	0.02
Trees thin	7.89	1.30	10.13	1.34	1	0.06	1.61	0.08
Logs decay 2	4.27	0.73	5.27	0.86		0.11	1.48	0.12
Stumps decay 5	0.69	0.15	0.42	0.13		–0.4	–1.38	0.13
Stumps decay 4	1.33	0.31	0.91	0.20		–0.2	–1.25	0.18
Stumps decay 3	0.89	0.14	1.18	0.25		0.23	1.17	0.23
Logs decay 5	2.11	0.40	1.62	0.42		–0.13	–1.13	0.24

D. Travel sites

Variable	Avail. mean	SE	Used mean	SE	Correlate group[a]	Coeff.	Wald	P^b
Snags decay 3/4	0.81	0.25	1.35	0.30	1	0.52	2.34	0.01
Trees medium	1.23	0.22	2.37	0.46		0.27	2.19	0.01
Snags thin	1.16	0.32	1.86	0.43	1	0.34	1.90	0.02
Snags	1.81	0.37	2.54	0.43	1	0.21	1.79	0.05
Logs decay 4	2.44	0.37	3.23	0.52	2	0.13	1.56	0.10
Canopy	60.00	2.31	57.22	2.29		–0.03	–1.51	0.11
Stumps decay 4	1.30	0.28	0.96	0.17		–0.23	–1.32	0.15
Logs decay 2	5.51	0.93	4.65	0.80		–0.07	–1.29	0.18
Logs decay 3	4.39	0.59	3.74	0.55	2	–0.08	–1.15	0.24

[a] Correlate group includes variables that are related at Spearmean's rho ≥ 0.5. [b] Significance was obtained using the log likelihood ratio test.

Table 2.4. Coefficient estimates and diagnostic values from 1–1 matched case–control multiple logistic regression models that explain patterns of resting, foraging, scent marking and traveling by American marten in a young deciduous forest in northern British Columbia.

	Coefficient	SE	Wald	–2 Log Likelihood	Deviance	P^a
A. Resting dens						
Shrub cover %	0.31	0.18	1.75	41.59	8.32	0.004
Snags PCA factor 1	3.14	1.88	1.67	35.98	5.61	0.02
Stumps decay 3	1.24	0.66	1.88	31.16	4.81	0.03
Stumps short	–1.42	0.83	–1.71	25.35	5.82	0.02
Rootballs	2.24	1.41	1.60	21.72	3.62	0.06
Logs decay 2	1.33	0.79	1.69	19.51	2.22	0.14
Logs decay 2 x shrub cover %	–0.04	0.03	–1.42	16.04	3.47	0.06
B. Subnivean foraging sites						
Logs PCA factor 1	0.85	0.48	1.77	64.16	6.54	0.01
Snags decay 3/4	0.69	0.34	2.03	55.27	8.89	0.002
Stumps PCA factor 1	–2.01	0.86	–2.34	50.73	4.54	0.03
Stumps PCA factor 2	0.93	0.52	1.79	46.02	4.71	0.03
Snags decay 3/4 x Stumps PCA factor 1	–0.77	0.44	–1.75	41.86	4.16	0.04
C. Scent marks						
Logs decay 2	0.17	0.09	1.85	59.95	2.44	0.12
Trees thin	0.07	0.04	1.74	56.28	3.66	0.06
Trees wide	0.89	0.53	1.69	49.79	6.49	0.01
D. Travel sites						
Snags PCA factor 1	1.22	0.59	2.05	72.53	6.49	0.01
Logs decay 3	–0.13	0.08	–1.59	69.70	2.84	0.09
Stumps decay 4	–0.56	0.26	–2.11	66.45	3.25	0.07
Trees medium	0.36	0.17	2.12	60.28	6.17	0.01

[a] **Significance was obtained using the log likelihood ratio test.**

Table 2.5. Eigenvectors and eigenvalues extracted using principle components analysis from habitat variables that were significant in preliminary multivariate 1–1 case control logistic regressions and were correlated at Spearman's rho ≥ 0.5.

A. Resting dens snags

Variable	Factor 1	Factor 2
Snags	0.97	–0.18
Snags thin	0.87	–0.49
Snags medium/wide	0.64	0.75
Snags decay 5/6	0.91	0.13
Eigenvalue	2.94	0.85
Total variance explained = 94.50 %		

B. Subnivean foraging sites logs

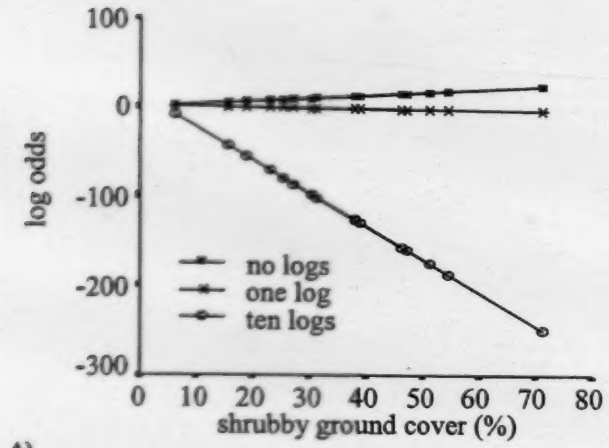
Variable	Factor 1
Logs	0.86
Logs medium	0.89
Logs suspended	0.88
Logs decay 2	0.92
Total logs	0.94
Eigenvalue	4.02
Total variance explained = 80.35%	

C. Subnivean foraging sites stumps

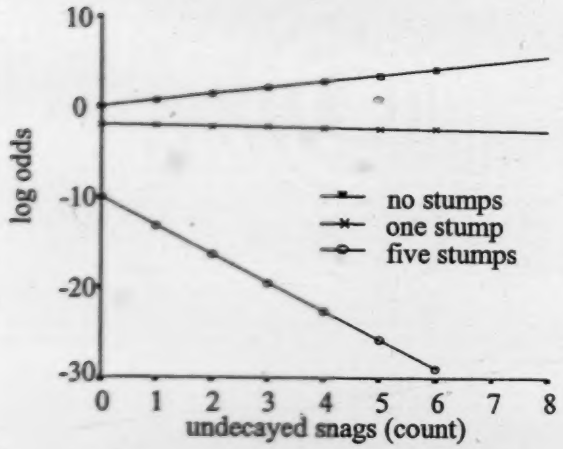
Variable	Factor 1	Factor 2
Stumps thin	0.84	–0.33
Stumps wide	0.20	0.96
Stumps tall	0.89	–0.02
Stumps decay 3	0.86	0.12
Eigenvalue	2.28	1.05
Total variance explained = 83.28%		

D. Travel sites snags

Variable	Factor 1
Snags	0.96
Snags thin	0.97
Snags decay 3/4	0.94
Eigenvalue	2.75
Total variance explained = 91.66%	



A)



B)

Figure 2.1. Interaction terms that predict habitat use by American marten living in a young deciduous forest in northern British Columbia. A) The logit of the probability of resting relative to the density of shrubby ground cover at three different levels of freshly fallen logs. B) The logit of the probability of foraging relative to the number of undecayed snags in a sample plot at three different levels of thin stumps.

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CHAPTER THREE – HABITAT SELECTION BY AMERICAN MARTEN (*MARTES AMERICANA*) IN A YOUNG DECIDUOUS FOREST IN NORTHERN BRITISH COLUMBIA

American marten are the most commercially important furbearers in parts of Canada (British Columbia Ministry of Environment, Lands and Parks 1997; H. Slama, Department of Renewable Resources, Government of Yukon, personal communication) and are sensitive to the effects of forest harvesting (Baker 1992, Buskirk and Powell 1994, Chapin et al. 1998, Potvin et al. 1999) such that they have been extirpated from parts of eastern Canada and nine northern states as a result of the combined effects of habitat loss and overtrapping (Thompson 1991). Relative to many other forest–associated mammals, marten have large spatial requirements, low population densities and low reproductive rates (Buskirk and Ruggiero 1994, Payer and Harrison 1999). By identifying the habitat characteristics that are necessary for marten, managers will be in a position to protect this resource and may simultaneously protect other forest–adapted species.

Marten have been closely associated with forests containing the vertical and horizontal structural complexity that is most characteristic of older coniferous systems (Buskirk and Powell 1994, Drew 1995, Poole and Stanley 1998). Accumulated coarse woody debris is believed to provide good habitat for small mammal prey, access to these prey in winter, and shelter from predators (Martin 1987, Coffin 1994, Thompson and Curran 1995, Paragi et al. 1996). Wide diameter and moderately decayed deadwood, in particular, is necessary for insulated den sites in cold weather (Steventon and Major 1982, Coffin 1994, Bull and Heater 2000, Wilbert et al. 2000). Wide diameter live trees also provide den sites but usually during warmer weather (Bull and Heater 2000, Wilbert et al. 2000). Overhead cover and vertical structure, such as well distributed tree stems, are important for predator avoidance and escape (Baker 1992, Coffin 1994, Drew 1995, Potvin et al. 2000). These resources may take decades to develop and some researchers believe that second growth forests provide marten habitat of lower quality (Buskirk and Powell 1994, Sturtevant et al. 1996).

Despite this strong association with older forest systems, a recent study detected a population of American marten living in a distinctly different habitat type in northern British Columbia (Grindal et al. in review). The Rice Property is dominated by a young deciduous forest and at least one third of the area is classified as open habitat. With the exception of stands that retain abundant debris following a natural disturbance (Paragi et al. 1996, Chapin et al. 1997), marten avoid regenerating forest and open areas (Coffin 1994, Drew 1995, Payer and Harrison 1999, Potvin et al. 1999). For these reasons, the Property was given a low ranking by the locally–developed habitat suitability model.

I examined the aspects that appear to make this study system suitable for marten. I detected habitat selection by marten in this area for resting and foraging sites at a very small scale (element scale as defined by Weir 1995; Chapter Two this volume). In this second component, I wished to investigate whether and how these small scale results translate into the patch and stand scales that are more typically used by managers. While marten may use the area unselectively, there are remnant stands of older forest that may provide core areas of higher quality. Alternatively, young forests have been found to contain structural features remnant from the previous old growth stands (Chesterman and Stelfox 1995) and this may be the case here. My objective was to determine if marten were using the Rice Property selectively at the stand or patch scales (*sensu* Johnson 1980) and, if so, to describe the features that were most important. Although marten are known to react adversely to forest harvesting (Thompson and Harestad 1994), management options will be broadened if populations can be reestablished in younger forest stages.

STUDY AREA

This project was conducted on the Rice Property, a parcel of overgrown agricultural land, in Canada's boreal mixedwood forest, 40 km east of Chetwynd, British Columbia, Canada (121° 48' W and 55° 42' N). The Property itself covers 5880 ha, but telemetry locations extended the study area to approximately 7850 ha. About 5500 ha of the total area is now forested, with 90% composed of deciduous stands (*Populus tremuloides and P. balsamifera*) and the remainder dominated by conifers (*Picea spp., Pinus contorta*). Nearly 65 % of the total forest is under 60 years of age and 45 % is between 5 and 25 years. Small stands of mature aspen, mixed aspen/spruce and spruce and tamarack (*Larix*

larcina) bogs were left after the initial clearing. The nonforested land is mainly composed of pastures, clearings and wetlands. The entire area has been fragmented by seismic lines, gravel roads and trails, and clearings related to past agricultural use and timber harvesting. Debris piles and remnant live trees, stumps, logs and snags from the initial clearing are scattered through the younger forest stands.

METHODS

I used a resource selection function to detect habitat selection by marten at the patch and stand scale (Manley et al. 1993). This technique involves (1) identifying habitat that was *used* by marten at each of these scales, (2) identifying habitat that was *available* for the marten to use, (3) surveying the characteristics of the habitat at both these used and available sites, and then (4) applying a statistical comparison (logistic regression) to determine if marten were disproportionately using any of the habitat characteristics compared to their availability. I defined selection at the patch scale as the preferential use of one hectare sized patches of habitat compared to other one hectare sized patches that were randomly available inside the same forest stand. I defined the stand scale as the preferential use of particular forest stands as compared to their availability within the marten home ranges. Stands were delineated based on similar vegetation characteristics visible on mid-scale aerial photographs (1:15,000; British Columbia Ministry of Forests 2001a).

Radio telemetry

Radio collaring was conducted in December of 1998 by Axys Environmental Consulting Ltd. (Grindal et al. in review) and in November of 1999 by my field assistants and I. The methodology was similar in both years. The marten were trapped in Havahart Live Traps that were located along roads and trails. Each trap was lined with straw, placed inside a waxed cardboard box, and baited with 500 g of meat and half an apple. We left the traps open for 24 hours and checked them twice daily. We immobilized the animals with a 1:1 mixture of tiletamine:zolazepam (Telazol®) that was injected intramuscularly. While the marten were immobilized we fitted them with Holohil® (40 g) or Telonics® (50 g) radio collars. We classed them by sex (based on the presence of testes or vulva patch)

and age (based on the presence of a sagittal crest and the degree of tooth wear). The animals were also weighed, measured, ear tagged and given an antibiotic injection. We kept them warm using a wool blanket and warm water bottle and we protected their eyes with a lubricating ointment. After the procedure, we placed the marten back in the live trap until they were fully recovered. Thirteen marten were collared in 1998 (2 adult females, 8 adult males, 3 juvenile males) and 18 were collared in 1999 (7 females [5 adult, 2 juvenile], 11 males [8 adult, 3 juvenile]) including seven recaptures from the previous season.

We located the radio collared marten year around using standard ground telemetry procedures (Samuel 1996, British Columbia Ministry of Environment, Lands and Parks 1998). Bearings were taken from permanent ground stations that were positioned along roads and seismic lines or within cutblocks. A minimum of three bearings was taken for each radio location. I used LOCATE II (Nams 1990) to calculate the position of the animals. When there were more than three bearings, I eliminated any that appeared to be outliers, that had been taken from a faint or pulsing signal, or that were separated in time from the other locations (>0.5 hour). We did all the telemetry during daylight hours (0900h – 1900h) and monitored the marten systematically, when possible, so that sampling effort was evenly distributed among animals.

I then selected a subsample of the total radio locations to include in the analyses. The number of sites that I was able to sample for this analysis was limited by the time required to survey habitat characteristics on the ground. Thus, I randomly chose four to five replicate radio locations for each individual animal (total 61 sites: five adult females, nine adult males). A similar number of sites was used for each animal to ensure that no individual had a disproportionate effect on the outcome. All of these locations were taken in the winter, had less than one hectare of telemetry error (as estimated by LOCATE II) and were within the estimated 50 % contour interval of the harmonic mean home range. These criteria resulted in a set of the most accurate locations from within core habitat. Next, I used a geographic information system (GIS) application to select a set of random points such that each telemetry location (or used site) was paired with a random site located within the same forest stand type (ArcView 3.2). These random sites

were intended to provide a measure of available habitat within the forest stands used by the marten (Manley et al. 1993). We located both random and used sites on the ground, prior to habitat sampling (below), using a real – time differentially corrected geographic positioning system (Trimble Geoexplorer3®).

At the stand scale, the subsample of radio locations included all those with less than 10 ha of telemetry error (total of 539 sites: five adult females, 15 adult males). These radio locations were taken in both summer and winter. I was able to include a large number of radio locations in this analysis because I obtained habitat information from GIS databases rather than by time–consuming field surveys. However, the sample size was still not sufficient to analyze habitat selection by individual animals. Consequently I combined the radio locations of individual animals and analyzed habitat selection separately for adult males and adult females. My attempt to address the possibility that an individual may be disproportionately influencing the model results is described with the statistical methods (below). Use of the GIS databases also allowed me to generate enough random sites to accurately represent the available stand types (9000 sites for the males and 2500 for females). Available habitat was defined as habitat that fell within the boundary of the 95 % minimum convex polygon home ranges that were calculated for all adult individuals and then pooled by sex. As the study progressed, Canadian Forest Products Ltd. conducted three successive winters of silvicultural activity where they sheared to ground height young aspen stands on the study site. I accounted for this disruption by estimating home ranges separately for each year and by associating these home ranges with modified GIS databases.

One assumption of use/availability habitat studies is that the sample of used habitat is representative of the habitat actually used by the animal. This assumption may be violated if accurate radio locations are harder to obtain in some habitats than they are in others. On the Rice Property, I suspected that radio locations may have been harder to obtain in older habitats because these tended to have reduced road access and more undulating terrain than the younger habitats. However, I did not detect an increase in telemetry error as stand age increased (Fig. 3.1). Further, the radio locations selected for analysis at the patch scale (restricted to those with <1 ha of telemetry error) are

representative of the total number of radio locations (Fig. 3.2). For these reasons, I believe that the radio locations that we took on the Rice Property are an accurate estimate of the habitat used by the animals.

Habitat sampling

At the patch scale, we conducted vegetation and prey inventories in order to identify the habitat characteristics that were associated with habitat use in winter. The sampling protocol for vegetation inventory was similar to standard government procedures (British Columbia Ministry of Forests 2001b) and resulted in 40 independent variables for analysis (Table 3.1). First, we assessed overhead cover before leaf–out using a comparison chart (British Columbia Ministry of Forests 2001b), in a 0.04 ha circular plot centered on the sample site. We made this estimate from a kneeling position to approximate marten head height in winter and we included all features that could provide cover (e.g. tree trunks, logs, forest canopy). Then after snowmelt, we established two transects 24 m long and two m wide at each site. The first transect was placed in a random direction while the second was extended at an additional 90 degrees from the first. Within each transect; logs, snags and stumps were counted; measured for width at a standard location and assigned a decay class (five classes for logs and stumps, three classes for snags). In addition, we classed logs as being down or suspended and measured the suspended log angle with a clinometer. We then assigned a height class to the stumps (short, medium, or tall). We counted trees and measured their diameter at breast height (dbh) and identified them to genus. We measured the length, width and height of rootballs and debris piles (± 10 cm rootballs, ± 25 cm debris piles). Finally, percent ground cover was estimated separately for shrubs, herbs and grasses in a 1 x 1 m quadrat using the Braun–Blanquet system of classification (Mueller–Dombois and Ellenberg 1974). Three estimates were made (one plot at the far end of each of the transects, plus a third plot at their central intersection) and their results were averaged for each cover type.

We surveyed small mammal abundance at the patch scale in the summer of 2000. Logistical constraints limited this survey to a randomly selected subset of 18 of the sites (one site per marten) that were surveyed for vegetation characteristics. We placed five

multiple capture live traps (Tincat™) at each site: one in the center and four others at 10 m spacing in each of the cardinal directions. These traps were prebaited for two nights and then trapped on the following two nights. All captures were counted by species, weighed and released.

At the stand scale, I obtained information on habitat characteristics using two GIS databases: the Vegetation Resources Inventory (VRI; updated 2000) and the Forest Cover Inventory (updated 1996). Both databases were necessary because the VRI covered only a portion of the study area yet provided more detailed and current vegetation information. I organized these data into 14 variables for the VRI database and five variables for the Forest Cover Inventory (Table 3.2). We were not able to sample the small mammal population at this scale.

Statistical analysis

All data were analysed by multiple logistic regression modelling using SPSS (Version 9.0, SPSS Inc. 1998) and S–Plus 2000 (Professional release 1, Mathsoft Inc. 1998–99) software. Although logistic regression response variables are typically binary and mutually exclusive, this can include the classification of habitat as used (activity sites) or available (random sites; see also Manley et al. 1993). This approach has several advantages over more traditional habitat analyses. In particular, it is quantitative and predictive, can be used for both continuous and categorical independent variables, and allows assessment of linear, non–linear and interaction effects.

The patch–scale data were analysed using one–to–one matched case–control logistic regression (Schlesselman 1982, Hosmer and Lemeshow 1989). This technique has the same capabilities as conventional logistic regression, but has the added advantage of removing variability that could not be otherwise assessed by matching sample sites by a common variable believed to be associated with the outcome. In this study, activity sites were matched with their paired random sites in order to emphasize within–site variability (i.e. that between paired random and used sites) while minimizing among–site variability (i.e. that occurring among sites [random or used] in different forest types). This powerful technique can be thought of as a functional equivalent of a paired t–test for multivariate

analyses. Although it is infrequently used in wildlife studies, it is a common tool in the medical sciences.

I developed two multiple logistic regression models (one model for adult males and another for adult females) using the one–to–one matched case–control technique. In both cases I followed a series of model–building steps that were derived from multiple sources:

1) I conducted univariate regressions on all the habitat variables to create a subset of the most significant variables. These were then used as candidates for inclusion in the multivariate model (Hosmer and Lemeshow 1989). I considered a variable to be significant enough to include in this subset if the log–likelihood test produced a P value < 0.25. Hosmer and Lemeshow (1989) recommend using this large P value to retain variables that may become significant only after the effects of other variables have been taken into account in the multivariate analysis. I discuss in the text those variables that were significiant in the univariate regressions at $P \leq 0.1$ and which were not included in the multivariate regressions. Finally, univariate parameters were reported as significant only if the magnitude of their Wald value was ≥ 1. The Wald statistic is not recommended as a test of significance (Hosmer and Lemeshow 1989) but was used as a diagnostic of a disproportionately large standard error of the coefficient.

2) I then constructed trial multivariate models using the candidate variables identified in the univariate analyses. When these indicated that some highly correlated variables (Spearman's rho < 0.5) would be included, I combined the related variables with principle components analysis. I then used the resulting components as candidate variables for logistic regression in place of the initial variables they represented. This precluded the subjective removal of variables and allowed for a more complete interpretation of habitat structure present on the study site.

3) I used these candidate variables to construct the multivariate models. I first added the main linear effects using a forward stepwise procedure based on the log–likelihood ratio with $\alpha = 0.1$ for inclusion and 0.15 for retention (Hosmer and Lemeshow 1989). Again, variables were removed if the magnitude of their Wald value was less than 1. Secondly, I

added quadratic variables if both the x and x^2 values satisfied screening criteria (log likelihood $P < 0.1$, Wald $\geq |1|$). I limited the assessment of non linear effects to quadratics because of their simplicity and plausible biological relevance. Finally, I tested all two way interactions between the main effects variables and included them if they provided a significant improvement in fit ($P < 0.1$) and were biologically interpretable.

4) I adjusted estimates of variance to account for the inflated sample size that resulted from the use of telemetry locations as replicates instead of individual animals. To obtain more realistic estimates of the standard error around the coefficient, I bootstrapped both the univariate and the multivariate models. This technique involves resampling the data with replacement many times in order to determine the relative frequency of obtaining all values of the coefficient. This process appropriately inflates the standard error of the coefficients such that Type 1 statistical errors resulting from pseudoreplication are less likely (Mooney and Duval 1993, Fortin and Jacquez 2000). I excluded those variables whose standard errors increased until the absolute value of their Wald statistic was ≥ 1.

5) I calculated three statistics to assess the overall performance of the final model. The log–likelihood ratio test and a measure of the proportion of explained variance analogous to linear regression (R^2_L) were used to determine if the model predicted the outcome variable better than a null model (Hosmer and Lemeshow 1989). These are relative measures that compare fitted values under two models. Conversely, goodness–of–fit is used to determine if the predicted values are an accurate estimation of the observed values in an absolute sense. This is harder to determine with case–control logistic regression because the response variable equals one for all strata (Hosmer and Lemeshow 1989). Therefore, I ran the final models with regular logistic regression and calculated the Hosmer and Lemeshow goodness–of–fit statistic as a conservative estimate of model fit (Hosmer and Lemeshow 1989). It is conservative because the desired partitioning of variance within and among pairs of points is not possible, increasing the likelihood of Type 2 statistical errors.

These five steps were used to examine the vegetation variables, but only the initial univariate analysis, could be applied to the small mammal data. This is because small

mammals were only surveyed on a subset of the patch sites ($n = 18$). Again, I used one–to–one matched case–control logistic regression to assess the importance of each variable independently. I organized the data into four continuous variables because only two of the five species small mammal species sampled had a sufficient number of captures to be included in the analysis. These were: (1) total captures, (2) average weight (g), (3) number of red backed voles, and (4) number of deer mice. I assessed both linear and quadratic relationships with the outcome. I considered variables to be significant if they met the conditions listed above for the univariate analysis of vegetation data.

I analysed the stand scale data with conventional logistic regression (Hosmer and Lemeshow 1989). I did this because trial models, in which sample sites were paired by home range, indicated that the matched case–control technique did not improve the fit of the model. The conventional method provided a larger sample size because used and random sites were not paired. It also permitted use of conventional model diagnostics. I built separate multivariate models for adults of each sex using both vegetation datasets (Vegetation Resources Inventory and Forest Cover Inventory; total of four models). I pooled the data in this way because the sample size was insufficient to build reliable models for most individuals. The statistical techniques and criteria used at the stand scale were the same as those applied to the multivariate models built at the patch scale with two exceptions. First, some individuals were monitored for longer periods than others and contributed a disproportionate number of locations to the dataset. In order to ensure that no animal had an overly strong influence on the results, I excluded all the locations from one individual, constructed the model with the remaining locations, and recorded the change in the coefficient. I repeated these steps until all the animals had been excluded from model construction in turn and the resulting change in the coefficients had been recorded. I highlighted for discussion any coefficients that changed by more than 20 %. These steps were not necessary at the patch scale because I analysed an even number of sites for each animal. Second, use of conventional logistic regression instead of matched case–control permitted the assessment of model performance with another diagnostic. At the stand scale I calculated the same diagnostics that were used at the patch scale, (the log–likelihood ratio, R^2_L, and a Hosmer and Lemeshow goodness of fit

criterion) and the percentage of results that were correctly classified. The Hosmer and Lemeshow statistic is not conservative when calculated for regular logistic regression.

RESULTS

Patch scale

The candidate subset that was used to build the multivariate models contained 17 variables for females and 12 variables for males. Of these, overhead cover was the only variable that was highly significant ($P < 0.1$) and retained a low standard error (Wald > 1) after bootstrapping (Table 3.3A). Both sexes tended to use sites with 50 % more cover than was available randomly in the habitat but the sites used by females tended to be more dense than those used by males (20 % versus 15 %).

Overhead cover was also the only variable that was included in the multivariate regressions for both sexes (Table 3.4). The models were highly significant according to the log–likelihood test. They also performed adequately according to the Hosmer and Lemeshow goodness–of–fit test (females $P = 0.96$, males $P = 0.12$). Consistent with this result was the approximate proportion of variance explained by the models which was higher for females ($R^2_L = 0.21$) than for males ($R^2_L = 0.12$; Table 3.4). Thus overhead cover was important at this scale but the models were not able to account for the majority of habitat use on this study site.

Small mammal survey

At the patch scale, 360 trap nights resulted in 283 captures of small mammals. Five species were represented, but 95 % of the captures were of two important prey species for marten. These included red backed voles (*Clethrionomys gapperi,* 13.33 captures/100 trap nights, 17 g mean weight) and deer mice (*Peromyscus maniculatus*, 61.11 captures/100 trap nights, 15 g mean weight). We captured only 3 meadow voles (*Microtus pennsylvanicus*) at the patch scale even through this species made up 20 % of the captures for a concurrent study on the Rice Property the previous summer (Chapter Two this volume). While there was a 66 % increase in the number of red backed voles at used sites compared to random sites, this difference was not significant ($P = 0.24$). None

of the other variables tested were significant and all had effect sizes of less than 10 %: total captures ($P = 0.82$), average weight ($P = 0.23$) and number of deer mice ($P = 0.79$).

Stand scale

Based on the univariate analyses, seven variables for males differed between used and random sites at the stand scale (Table 3.3B). Among the variables tested from the forest cover database, only deciduous trees in the forest understory were significant. Marten selected for deciduous trees when treed sites were compared to open areas. When forest stands were described by the VRI database, males selected for both coniferous and deciduous trees in the forest canopy compared to sites with no canopy cover. The strength of the response was similar for each type of tree. Males selected for a second VRI habitat variable, vertical complexity of the forest canopy, when forested sites were compared to nonforested sites. However, they selected less strongly for this variable as structural complxity increased.

The remaining four VRI variables that distinguished used sites from random sites for males were highly correlated and are represented by two PCA factors (Table 3.5). The first factor explained 69 % of the variance in the data while the second factor explained an additional 27 %. I equated the first factor with the presence of younger forests because it represents three variables (canopy closure, count of live trees, and basal area) that were not present in stands below 5 years of age, were high in stands 5–50 years old, and then decreased in stands older than 50 years (Fig. 3.3). In contrast, the second factor corresponded to older forests because the single variable that it represented, volume of harvestable wood, was not detectable in stands below 30 years of age and then increased with age. Male marten used sites with 14 % more canopy cover, 12 % more live stems, 24 % greater basal area, and 55 % more volume than was randomly available. Selection for both these PCA factors suggests that marten used structural characteristics common to both young and old stands.

Two variables from the VRI database were significant in the univariate analyses for female marten: volume of harvestable timber and count of snags per hectare (Table 3.3B). Females tended to use sites with 60 % more volume and 140 % more snags than

were available randomly in the habitat. While the size of their response to volume was similar to that of males, females more often used denser sites (33 m^3/ha compared to 20 m^3/ha).

Highly significant multivariate models were built for both male and female marten using the Vegetation Resources Inventory database, and for males alone using the Forest Cover Inventory database (Table 3.6). Females used all the variables in the Forest Cover Inventory in proportion to their availability. Despite the significance of the variables that were included, all these models had low predictive success (average of 56 % compared to 50 % for a null model; Table 3.7) and explained a small amount of the deviance in the data (maximum $R^2_L = 0.02$). Males selected only for deciduous trees in the forest understory in the model built with the Forest Cover Inventory database (Table 3.8A). Using the VRI database, they selected for vertical complexity of the forest canopy and for the principle component that represented increasing volume of live trees per hectare (Table 3.8B). Females selected for both variables that were significant in their univariate analyses; higher counts of snags and greater volume of live trees in the forest canopy (Table 3.8C).

It is possible that I detected relatively little selection because marten were not highly selective of their habitat at this site and scale, or because variation in the habitat used by individuals masked my ability to detect consistent patterns of selection. To assess the potentially disproportionate effects of single individuals, I bootstrapped every individual. I found that six males had a large influence on the beta coefficients (> 20 %) for at least one variable. Although some individuals selected more strongly and others more weakly, all the variables retained their significance and the direction of the relationship (selection or avoidance) remained constant. The results were less straightforward for females. The model suggested that females generally selected for snags. Yet the removal of one female markedly increased this effect while the removal of another caused the model to predict avoidance of this same feature. This was also observed with the second variable that was significant for females: volume of harvestable timber.

DISCUSSION

Patch scale

At the patch scale, overhead cover was the only variable that distinguished the sites used by marten. None of the other vegetative characteristics traditionally associated with marten habitat were responsible for the observed patterns of habitat use at the patch scale in this uncharacteristic habitat type. This included measures of structural complexity (e.g. diameter, decay status and count of logs), tree age (represented by tree diameter) and tree species.

Both sexes tended to select sites with about 50 % more overhead cover than was available in the surrounding habitat. Marten presumably selected high cover values in order to avoid avian predation (Hargis and McCullough 1984, Lachowski 1997, Potvin et al. 2000). Females used sites with 20 % cover on average while males used sites with 15 % cover. This variable was highly significant ($P < 0.01$), but these estimates were lower than ones that have been detected elsewhere. Other studies found that marten avoided sites with < 30 % cover in winter (Koehler and Hornocker 1977) or even < 50 % (Hargis and McCullough 1984, Thompson and Harestad 1994). In addition, my cover estimates were higher than those conventionally collected because I measured the protection offered by all structures above the estimated height of a marten. In contrast, most studies sample only the forest canopy. Interestingly, cover was not observed to be important at either the larger (stand) scale in this study or at the smaller (element) scale (Chapter Two this volume). This suggests that marten perceive cover at a particular scale that is larger than individual structural elements, such as stumps or logs, but not as large as the stands outlined by managers.

An examination of the suite of diagnostic criteria used to build these models indicated that females were somewhat more selective than males in their habitat requirements at the patch scale. Telemetry locations taken for females are more likely to represent high quality habitat because females generally have smaller home ranges and travel less extensively than males do (Buskirk and Powell 1994). Females may have selected denser

habitats than males (20 % cover compared to 15 %) because of an increased risk of predation associated with raising young.

The patch scale models were highly significant. However, they also explained only a portion of the deviance in the data (21 % females, 12 % males). Taken together, these diagnostics indicate that marten were less specific about the habitat they used at the patch scale than they were in the element scale models (30 m resolution), especially for resting dens, that I described in Chapter Two. As I discuss in the next section, this suggests that marten on this study site may select their habitat at a very small scale.

Stand scale

The stand scale multivariate models were very significant ($P_{max} = 0.001$), but they explained 2 % or less of the deviance in the data and had low predictive success (56 % for all models compared to 50 % for a null model). This suggests that habitat selection was weak at the stand scale for both sexes. This is the first study to detect marten living so unselectively in an area with such a large amount of both nonforested (~25 %) and young deciduous habitats (~38 % less than 25 years old). An examination of the variables that were significant shows that marten preferred forested rather than open areas. However, consistent with the patch scale results, I detected only equivocal evidence that the study animals distinguished these forests by stand age or species.

Male marten selected both coniferous and deciduous trees in the forest canopy and deciduous trees in the understory. The animals showed nearly equivalent selection for each type of stand. Because these patterns were detected when open sites were compared with forested sites, it seems that forests provided better habitat for males than open areas. However, the species of tree in these forests did not appear to influence choice of habitat. Similarly, I did not detect an effect of forest type on habitat selection by females as they used both types in proportion to availability. These results suggest that the structural features necessary for marten were present in both coniferous and deciduous stands.

Age of the forest was not a significant influence on habitat selection by either sex. Instead, the animals reacted to a suite of structural features that were associated with age. Males selected for a high volume of harvestable wood (PCA factor two) in their

multivariate (VRI) model. Volume was detectable only in stands over 30 years of age and increased as the stands matured. However, these animals concurrently selected for canopy cover, count of live stems and total basal area (PCA factor one) all of which were most common in younger forests. Thus male marten selected for characteristics of both young and old stands rather than preferring older habitats alone. In contrast, female marten selected only for variables that were associated with older stands; higher volume of harvestable timber and counts of dead stems per hectare. Timber volume increased with stand age and over 95% of dead stems occurred in stands that were over 70 years old. Although females did not react to stand age as a variable, they were somewhat more likely to use older stands if they contained snags and harvestable volume.

It appears that younger as well as older forests have the structural features that are necessary for American marten. Marten are believed to require overhead cover to avoid predation (Hargis and McCullough 1984, Coffin 1994, Drew 1995). It is likely that this cover can be provided by the canopy and live stems in the dense stands of short trees common to early successional deciduous forests. However the effect size was small as the animals tended to use sites that had only 23 % more canopy and 15 % more live stems than were randomly available. While young stands on the Rice Property have approximately 80 % canopy cover and about 6000 live stems/ha, the marten used habitats that were only half as dense on average (Table 3.3D). This amount of canopy cover is similar to that found in other studies (Koehler and Hornocker 1977, Hargis and McCullough 1984, Thompson and Harestad 1994). Yet, to explain these results, marten must have selected higher canopy cover while also making frequent use of older and nonforested habitats with little or no canopy cover.

The volume of harvestable wood and the density of snags were both characteristic of older habitats. These systems are likely to have the complex structures, especially those with wide diameter and moderate decay class, that are generally characteristic of marten habitat. Overhead cover here may come from a dense understory shrub layer or downed woody material (Thompson and Curran 1995, Paragi et al. 1996, Chapin et al. 1997). The snags selected by females provide vertical structure that marten may use for elevated

den sites or escape from predation (Raphael and Jones 1997, Ruggiero et al. 1998, Wilbert et al. 2000).

The last variable that was important was the vertical complexity of the forest canopy. A more complex canopy contains a variety of trees of different heights and species and is an indicator of a more complex understory. Males selected for vertical complexity when forested sites (class 1–5) were compared with non–forested sites (class 0), but they showed progressively less selection as complexity increased. Yet the marten–require–structural–complexity paradigm asserts that more complex habitats are preferable to less complex ones, which was not detected in this study. On the Rice Property, marten showed the strongest selection for class one complexity which corresponded to a very uniform canopy of immature poplar stands (British Columbia Ministry of Forests 2001a). This result was also inconsistent with the idea that marten require older or coniferous forest.

These habitat characteristics explained only a fraction of habitat use, for both female and male marten. Yet females often used stands that had more harvestable timber and that tended to be slightly older than those used by males. In combination with the higher selectivity detected at the patch scale, this suggests that female marten on the Rice Property used higher quality habitats than those used by males. Females are likely to be more specific because they have the added demands of raising young.

Examined together, all of the selected features depict marten simply as a forest–adapted species, rather than one that selects old growth or coniferous forests in particular. This is especially evident from the variables selected by males at the stand level: both young and old stands, both deciduous and coniferous vegetation, and all levels of vertical complexity. I believe this pattern emerged because the open habitats on this study site were so extensive (25 %) that a slight avoidance of these areas by marten could have exerted a strong influence on the analysis. Yet despite this slight avoidance, the low selectivity detected at the stand scale overall indicates that both sexes frequently used young forests and open areas; habitats that heretofore they have almost always selected against (Coffin 1994, Drew 1995, Payer and Harrison 1999, Potvin et al. 1999).

Despite their avoidance of nonforested areas, marten do use open habitats more commonly in the summer when low growing shrubs can provide overhead cover (Koehler and Hornocker 1977, Steventon and Major 1982). I assessed only winter habitat use at the patch scale, but in order to have a strong sample size at the stand level, I combined telemetry locations taken in both winter and summer. Thus, use of open and young habitats may have occurred after leaf out. Forty percent of the open areas that were inventoried by the VRI (10 % of the 5880 ha covered by this database) were composed of shrub habitats that may have served in this way. The Forest Cover database, which inventoried the entire study area, does not provide this information.

Animals use low quality habitats for a number of reasons (Van Horne 1983) but these habitats are likely to be population sinks (e.g. Bryant 1999). I do not have a direct estimate of reproductive success for marten on the Rice Property, but surrogate measures indicate that it is not a sink habitat. These measures were calculated yearly between December of 1998 and February of 2002 (Grindal et al. in review, Poole and Maundrell 2002). During this time, early winter (Nov–Dec) trapping success was consistently high (4.1–5.7 individuals/100 trap nights, density of 0.24–0.37 marten/km^2), the proportion of males (47–72 %) and juvenile animals (0–41 %) was reasonable, and annual home range sizes were on the low end of those reported for marten elsewhere in North America (Burkirk and McDonald 1989, Powell 1994; 95 % minimum convex polygon for males 2.16–2.41, females 0.70–1.68). Thus, the Rice Property appears to be able to sustain a viable population of marten at least in the short term.

Patterns of habitat selection that are detected at one spatial scale will not necessarily represent selection that occurs at a different scale (Bissonette 1997). Many researches believe that multiscale studies are necessary to obtain a more complete understanding of habitat selection (Orians and Wittenberger 1991, Labbe and Fausch 2002). While little selectivity was detected at the stand scale in this study, marten were selective for overhead cover at the patch scale. They were even more specific in the concurrent element scale project (resolution of 30 m) that detected strong patterns of selection that were linked to particular behaviours (Chapter Two this volume). Thus it is possible that habitat selection was not detected at the stand scale because it was occurring at a smaller

scale or because it was obscured by the divergent habitat needs associated with particular behaviours (e.g. denning vs. traveling). These results suggest that marten may select habitat in ways that would be difficult to detect at the larger scales of investigation that typify management contexts.

Marten may be able to meet their habitat requirements in more ways than has been previously thought. However, there are some limitations of the modeling process that may have contributed inappropriately to this conclusion. One shortfall is that stand scale information on deadwood, except for snag count, was not available. Coarse woody debris in particular has been found to be very influential on habitat selection by marten (Steventon and Major 1982, Corn and Raphael 1992, Coffin 1994, Thompson and Curran 1995) and other forest animals (Bull et al. 1997). In fact, marten have even been detected in younger forests that retained abundant deadwood following disturbance by fire (Paragi et al. 1996) and insect outbreaks (Chapin et al. 1997). In contract, marten tend to avoid forests the are regenerating after clearcutting partially because these are likely to be lower in coarse woody debris (Thompson and Harestad 1994). Most of the arable land on the Rice Property was cleared for agriculture and the debris was piled and left (Grindal et al. in review). For this reason the young stands on this site probably retained more debris than a clearcut habitat, but it would be distributed in a more clustered manner than following a natural disturbance. Information on coarse woody debris is rarely available in the stand scale databases used by forest managers. Rather, it is usually assumed that variables such as stand age and species are reliable indicators. This assumption may not always be valid and, because of its biological relevance, I recommend that these databases be expanded to include information on coarse woody debris.

Another consideration for interpreting my results is that I based this analysis on the average selection of individuals, but later showed evidence for females that different directions of selection were cancelling each other among individuals. Accordingly, the variables that I identified were not necessarily important for all individuals while I may have overlooked variables that were key for particular marten. When possible, individuals should be used as the unit of replication rather than telemetry locations so that these effects can be identified.

In summary, this study suggests that young deciduous forests, potentially even those with substantial patches of nonforested land, can meet the habitat needs of marten at least in the short term. This implies that marten have more flexibility in habitat use than is generally assumed of this species. Given the consistent association between marten presence and structurally complex habitats, the use of young stands and open areas may be partially explained by habitat characteristics that were not available for this analysis, especially coarse woody debris. These habitats may have also been used more frequently in summer when shrubs can provide overhead cover. I found that marten were selective at a smaller scale for their den and foraging sites (Chapter Two this volume) and that they required overhead cover at the patch scale. It is possible that these animals were able to live in the younger forest stands because they were selecting the habitat they used in a more detailed way than could be detected in the stand scale analysis.

Table 3.1. Habitat variables measured at the patch scale to explain patterns of habitat use by American marten in a young deciduous forest in northern British Columbia.

Variable	Definition
Logs	diameter > 7.5 cm at widest point, length ≥ 1 m
thin, medium, wide	thin (< 10 cm), medium (10–25 cm) and wide (> 25 cm) diameter at widest point
grounded	laying flat on the ground
suspended	suspended off of the ground
angle	average angle to the horizontal of suspended logs
decay (class 1–5)	1 (fresh) to 5 (completely rotten)
Stumps	top diameter ≥ 4 cm, height ≤ 1.5 m
thin, medium, wide	thin (< 10 cm), medium (10–25 cm) and wide (> 25 cm) diameter across the top
short, medium, high	short (< 0.5 m), medium (0.5 m – 1.0 m), and high (1.0 m – 1.5 m)
decay (class 1–5)	1 (fresh) – 5 (completely rotten)
Snags	standing dead tree, height > 2 m, diameter at breast height ≥ 4 cm
thin, medium, wide	thin (< 10 cm), medium (10 – 25 cm) and wide (> 25 cm) diameter at breast height
decay (class 3/4, 5/6)	combined decay classes from 3 (fresh) to 6 (rotten)
Trees	height > 2 m, dbh ≥ 4 cm
thin, medium, wide	thin (<10 cm), med (10–25 cm) and wide (> 25 cm) diameter at breast height
deciduous, coniferous, shrubby	deciduous (*Populus, Betula*), coniferous (*Pinus, Picea*) and shrub (*Alnus, Salix*) form trees
Grass, shrub, herb	average percent cover ground cover
Rootballs	mound of dirt and root at the base of a fallen tree
Overhead cover	% cover measured at 1 m above ground

Table 3.2. Habitat variables that were extracted from the Vegetation Resources Inventory and Forest Cover Inventory databases in order to explain stand scale patterns of habitat use by American marten. All variables from the VRI dataset except canopy and volume apply to both the overstory and understory forest layers. The FCI was limited to the primary forest layer for all variables.

Variable	Database	Definition
Canopy[a]	VRI and FCI	vertical projection of forest canopy
Basal area (m^2 per ha)	VRI	total cross sectional area, at breast height, of all trees
Live stems (per ha)	VRI	count of trees > 4 cm diameter at breast height
Dead stems (per ha)	VRI	number of standing dead trees
Vertical complexity (1–5)	VRI	describes the form of each tree layer from 1(very uniform) – 5 (very non–uniform)
Age	VRI and FCI	average for the leading and second species of each layer
Primary species (deciduous, coniferous)	VRI and FCI	species that occupies > 50 % of the layer
Secondary species (deciduous, coniferous)	FCI	species that occupies < 50% of the layer
Volume (per ha; layer 1)[a]	VRI and FCI	volume of trees > 10 cm diameter at 30 cm from the ground

[a]Variables tested only for the primary forest layer.

Table 3.3. The mean, standard error, coefficient and model diagnostics of habitat variables found to have a linear relationship with the outcome in 1–1 matched case–control *univariate* logistic regressions. These variables partially explain habitat selection by American marten in a young deciduous forest in northern British Columbia.

A. Patch scale

Variable	Avail. Mean	SE	Used Mean	SE	Coeff.	Wald	Devi–ance	P[a]
Males								
Overhead cover %	10.45	1.54	15.45	2.04	0.06	2.03	6.53	0.01
Females								
Overhead cover %	13.41	1.37	19.90	2.41	0.14	1.68	6.29	0.01

B. Stand scale

Variable	Avail. Mean	SE	Used Mean	SE	Coeff.	Wald	Devi–ance	P[a]
Males – Forest Cover Inventory								
Understory species[b,d]								
Deciduous					0.51	2.43	26.37	<0.001
Males – Vegetation Resources Inventory								
Vertical complexity layer 1[b,c]							52.72	<0.001
Code 1					2.28	4.07	13.72	<0.001
Code 2					1.05	4.50	4.37	0.04
Code 3					1.01	4.56	31.01	<0.001
Code 5					0.63	1.93	4.13	0.04
Overstory species[b]							38.91	<0.001
Deciduous					1.02	4.86	26.99	<0.001
Coniferous					0.91	3.08	11.59	<0.001
Factor 1 layer 1					0.20	3.33	14.64	<0.001
Canopy	41.18	0.42	47.24	1.69				
Live stems	3522.74	41.63	3954.73	184.79				
Basal area	12.74	0.14	15.75	0.66				
Factor 2 layer 1					0.13	2.60	7.36	0.007
Volume	13.41	0.40	20.59	2.32				
Females – Vegetation Resources Inventory								
Dead stems	5.69	0.48	13.55	4.20	0.02	1.02	4.80	0.028
Volume	20.40	0.83	32.83	5.88	0.01	1.52	8.08	0.004

[a]Significance was obtained using the log likelihood ratio test. [b]The coefficients for the categorical variables reflect the strength and direction of habitat selection when forested sites were compared to sites without forest cover. [c]The Code 4 comparison for vertical complexity was omitted because it was absent from the study site. [d]Species were classed as dominant deciduous or dominant coniferous. Statistics for coniferous stands in the forest understory are not listed because this variable was not significant.

Table 3.4. Coefficient estimates and diagnostic values from 1–1 matched case–control *multiple* logistic regression models that explain patterns of *patch* scale selection by American marten in a young deciduous forest in northern British Columbia.

	Variable	Coeff.	SE	Wald	Deviance	P^a	C^2	P^b	R^2_L
Males	Overhead cover %	0.07	0.03	2.14	6.53	0.01	10.23	0.12	0.12
Females	Overhead cover %	0.14	0.08	1.75	6.29	0.01	1.57	0.96	0.21

[a] Significance of the log likelihood value that was used to assess how much better the multivariate model predicted the outcome variable than did the null model. [b] Significance of the Hosmer and Lemeshow goodness–of–fit statistic (C) that was used to assess how well the multivariate model predicted the outcome value in an absolute sense. For this second test, models are considered to be adequate when $P > 0.05$.

Table 3.5. Principle component analysis used to combine several related variables from the Vegetation Resources Inventory database for male marten.

Variable	Factor 1	Factor 2
Canopy layer 1	0.98	–0.10
Basal area layer 1	0.95	0.17
Live stems layer 1	0.91	–0.38
Volume layer 1	0.29	0.95
Eigenvalue	2.78	1.09
Percent variance explained	69.18	27.41

Table 3.6. Overall model fit diagnostics for 1–1 matched case–control *multiple* logistic regressions that explain observed patterns of *stand* scale habitat use by American marten in a young deciduous forest in northern British Columbia.

		–2 Log likelihood	Deviance	P^a	C	P^b	R^2_L
Males	FCI	3424.58	28.36	<0.001	NA[c]	NA[c]	0.01
	VRI	2666.73	59.56	<0.001	0.11	0.99	0.02
Females	VRI	788.31	13.28	0.001	3.28	0.51	0.02

[a] Significance of the log likelihood value that was used to assess how much better the multivariate model predicted the outcome variable than did the null model. [b] Significance of the Hosmer and Lemeshow goodness–of–fit statistic (C) that was used to assess how well the multivariate model predicted the outcome value in an absolute sense. For this second test, models are considered to be adequate when $P > 0.05$. [c] These statistics can not be calculated for this model because it does not have enough covariate patterns (Hosmer and Lemeshow 1989).

Table 3.7. The percent correctly classified by three logistic regression models that partially explain patterns of *stand* scale habitat selection by American marten in a young deciduous forest in northern British Columbia.

	Predicted available	Predicted used	Percent Correct
Available	6283	2209	74.0
Used	267	164	39.0
Average percent correct			56.0
Available	5488	1720	76.1
Used	209	122	36.9
Average percent correct			56.0
Available	2109	302	87.5
Used	72	22	23.4
Average percent correct			56.0

Table 3.8. Coefficient estimates and diagnostic values from multiple logistic regression models that explain patterns of stand scale selection by American marten in a young deciduous forest in northern British Columbia.

Variable	Coefficient	SE	Wald	–2 Log Likelihood	Deviance	P^a
A. Males Forest Cover						
Species layer 2						
Deciduous	0.55	0.22	2.46	3424.58	28.36	<0.001
B. Males VRI						
Vertical complexity layer 1[b]				2663.76	52.72	<0.001
Code 1	2.35	0.54	4.35			
Code 2	1.05	0.23	4.50			
Code 3	0.95	0.22	4.29			
Code 5	0.63	0.34	1.87			
Volume layer 1	0.13	0.04	2.89	2656.92	6.84	0.011
C. Females VRI						
Dead stems	0.01	0.01	1.08	795.05	6.54	0.03
Volume layer 1	0.01	0.01	1.27	788.31	6.74	0.02

[a] Significance was obtained using the log likelihood ratio test. [b]The vertical complexity coefficients reflect the strength and direction of habitat selection when forested sites (codes 1–5) were compared to sites without forest cover (unclassed). The Code 4 comparison was omitted because it was not common on the study site.

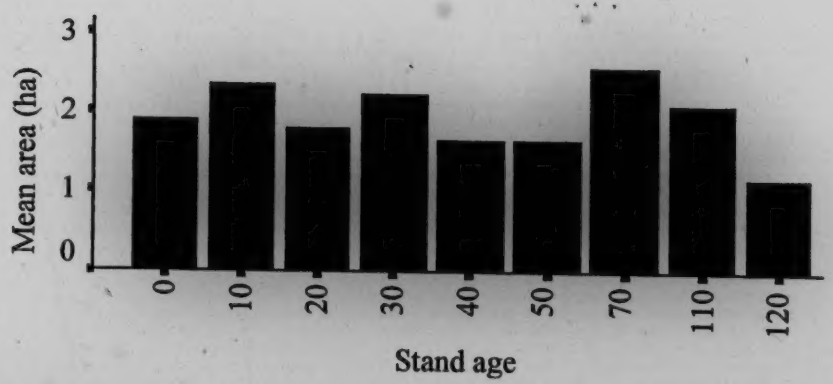

Figure 3.1. Mean area of the polygon of telemetry error around radio locations as age of forest stands increases. There were no stands of 60 or 80–100 years on the Rice Property at the time of the study. These locations were taken on American marten in a young deciduous forest in northern British Columbia.

Figure 3.2. Distribution of sample sites at the patch and stand scales in relation to forest stand age for a population of American marten in a young deciduous forest in northern British Columbia.

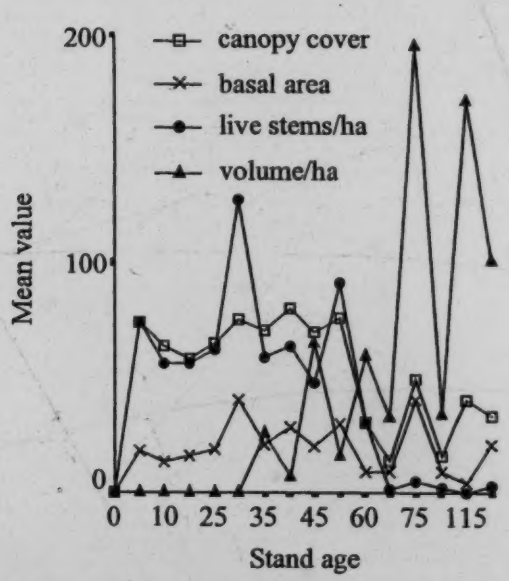

Figure 3.3. The mean values graphed by forest stand age of four independent variables from the VRI database that significantly distinguished used from random sites for adult male marten living in a young deciduous forest in northern British Columbia.

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CHAPTER FOUR – CONCLUSIONS

Forest managers must increasingly balance the needs of industry with the public's growing appreciation of wild plants and animals (Adamowicz and Codon 1997, Boutin and Hebert 2002). A clear understanding of the habitat requirements of sensitive species is an important stepping stone to making management choices that will meet the expectations of both these groups. I conducted a multiscale habitat study on a population of American marten that was detected living in an atypical habitat type (Grindal et al. in review). Marten are important to industry because they are important furbearers and are sensitive to the effects of habitat loss and fragmentation (Hargis et al. 1999). Marten are strongly associated with structurally complex habitats, especially late successional coniferous forests that are targetted by industry (Buskirk and Powell 1994). In contrast, my study area was dominated by young deciduous forest. In this thesis, I attempted to resolve this discrepancy by investigating habitat selection at three spatial scales: element, patch and stand. After the Introduction (Chapter One), Chapter Two focused on element scale selection for specific activities. Then, Chapter Three examined the patch and stand scales that are more commonly used by management. The purpose of the concluding chapter is to synthesize the importance of these results to managers.

Two major patterns emerged from the element scale analysis. First, marten selected their habitat differently for each of four different activity types: denning, foraging, scent marking and traveling. Of the habitat variables incorporated into the models, only 1/5 were selected similarly (either selected or avoided) for more than one purpose. This suggests that each activity is done more effectively in a specific habitat. Managers and researchers should be aware that the particular resources that are necessary for some activities, but not for others, may not be detected in a study that does not take activity into consideration. Although this type of detail may be too specific for the kind of study that industry can be expected to support, it could be important when conventional studies present confusing information. It may be especially useful for wide ranging species, such as bears (Mauritzen et al. 2001) or caribou (Szkorupa 2002), that may disperse activities between different stand or even forest types. I suggest that future studies could profitably investigate activity–specific selection in even greater detail. This could be done by

resolving the habitat required by different individuals (e.g. males or females) or for different types of denning (e.g. natal, maternal) or foraging (e.g. predatory, harvesting) behaviours.

The second conclusion of the element scale analysis is that the study animals were more selective for some activities than for others. They selected most strongly for resting dens, followed by subnivean foraging sites and were less selective of their scent mark locations and of their travel sites. This order may reflect the fitness consequences of selecting particular habitat for each activity; appropriate resting dens may be critical for the survival of a small mammal with little body fat (Buskirk et al. 1988) whereas travel sites may be expected only to optimize routes between resources. The stronger selectivity for resting and foraging suggests that the resources required for these activities are the ones that are most likely to limit population size. An effective habitat conservation plan should understand and meet the habitat needs of these activities in particular. The reduced selectivity detected at travel sites suggests that marten can move though less favourable areas in order to access smaller habitat patches. For marten in the boreal forest, such movement is more likely to occur once the forest has begun to regenerate (25 years for aspen/cottonwood stands; D.Rosen, Inventory Supervisor, Canadian Forest Products Ltd., personal communication). This vagility and flexibility should allow them to co–exist more successfully with the habitat fragmentation caused by land use activities such as forestry. This study did not determine the necessary quantity or distribution of the remnant patches necessary for foraging and resting. Future research should address this shortfall because these characteristics will affect patterns of habitat occupancy (Potvin et al. 1999).

Marten selected for a host of vegetation variables at their activity sites. In particular, they rested in areas that had higher densities of shrubs and freshly fallen logs that provided cover close to the ground. They also selected for many variables related to deadwood. At their resting dens, marten selected for moderately decayed stumps, wide diameter logs, and snags of all diameter classes. These structures have characteristics that allow them to provide shelter from inclement weather and predation (Buskirk 1984). At their foraging sites, marten selected for moderately decayed logs (as defined by British

Columbia Ministry of Forests 2001) with a medium (> 10 cm) to wide diameter (> 25 cm). The logs may provide protection from overhead predation (Drew 1995, Chapin et al. 1997), access to the subnivean hunt zone, and habitat for small mammal prey (Corn and Raphael 1992, Sherburne and Bissonette 1994).

This type of wide–diameter and moderately–decayed deadwood must be supplied in managed forests. Depending on their origin, young forests may have structural features remnant from the previous old growth stands. However, this material decays and is not replaced until the stand reaches old age (Chesterman and Stelfox 1995). The Rice Property was originally cleared for agriculture but retains debris piles and islands of large stumps, snags and logs that may be comparable to young stands of natural origin. Thus, the habitat suitability of this area is predicted to decline over the next 25–50 years. As forest rotation age for aspen mixedwood does not allow trees to senesce naturally (Chesterman and Stelfox 1995), complex systems will become progressively less common unless they are purposefully maintained or simulated by management (Angelstam, personal communication; Sturtevant et al. 1996).

In Chapter Three, I assessed habitat selection at the patch scale by adult marten of each sex. Both models performed adequately although females selected with marginally greater strength, possibly because of the higher demands associated with the rearing of young (Paragi et al. 1996). Overhead cover was the only vegetation variable that was important for either sex. Cover was not observed to be important at either the stand scale or at the element scale in this study. This suggests that marten perceive cover at a particular scale that is larger than individual structural elements, such as stumps or logs, but not as large as the stands outlined by managers.

At the stand scale in Chapter Three, I found that habitat selection was very weak for both adult males and females. This is the first study to detect marten living mostly unselectively in an area with such a large amount of both nonforested (~25 %) and young deciduous habitats (~38 % less than 25 years old). The vegetation variables that were significant suggest that marten prefer forested to open habitats. However, they selected some variables that are characteristic of young stands on the Rice (dense canopy, number

of live stems and total basal area) and others that are more common to older forests (volume of harvestable wood). They also showed equivalent selection for deciduous and coniferous trees in the forest overstory. Thus, I did not detect a dependence on either older or coniferous forests.

This lack of selection at the stand scale suggests that marten are able to use young forests, at least in the short term. Given the consistent association between marten and structurally complex habitats (Koehler and Hornocker 1977, Buskirk and Powell 1994, Coffin 1994, Payer and Harrison 1999), the use of these young stands may be partially explained by habitat characteristics that were not available for this analysis, especially coarse woody debris. Following clearing for agricultural purposes, logs and other remnants may have been distributed in such a way that their presence was not accurately represented by other stand scale measures. In fact, managers often rely on variables such as stand age and species with the assumption that they are adequate indicators of the available deadwood. This assumption may not be accurate because the deadwood characteristics of a stand tend to vary according to its origin (e.g. size and intensity of fire, duration of insect infestation, type of human disturbance; Chesterman and Stelfox 1995). Given the importance of deadwood to marten and other forest animals, stand scale vegetation inventories should contain this information. Unfortunately deadwood inventories are currently difficult to obtain remotely and ground surveys are time consuming. However, forest managers can survey deadwood in plots that are established within a set of representative stands. These plots should be monitored in the long term to ensure that deadwood characteristics do not change through repeated harvesting cycles.

Despite the lack of information on deadwood, the stand scale results imply that marten have more flexibility in habitat use than is generally associated with this species (Burkirk and Powell 1994). The patterns of selection detected at the patch and element scales suggest that marten may be able to live in the younger forest stands because they can find and travel between specific structural features that they use for particular activities. Thus it may be possible that habitat selection was not detected at the stand scale either because it was occurring at too small a scale or because it was obscured by the divergent habitat needs associated with particular behaviours (e.g. denning vs. traveling). These results

indicate that marten may select habitat in ways that would be difficult to detect at the larger scales of investigation that typify management contexts. It follows that habitat studies should be conducted across a range of spatial scales.

In this study I have shown that marten (1) use young forests and (2) select habitat at small spatial scales with greater intensity for some activities than for others. But I have not shown the fitness implications of these choices. This is rarely done in wildlife research because animals tend to be expensive to study and have long lives with low reproductive output. Density based studies are founded on the assumption that the highest quality habitat will be used most often. This assumption has been questioned (Van Horne 1983, Rosenzweig 1991). While animals are expected to select the highest quality habitat available to them (Manley et al. 1993), many other characteristics of both habitats (e.g. recent history) and animals (e.g. territoriality) confound the relationship between population density and habitat quality. Future research should compare reproductive success of animals living in different stand types and also between animals using different structural features for specific activities.

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